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Systematic Anatomy of the Woods of the Tiliaceae

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CONTENTS

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INTRODUCTION

WITHIN the last 20 years there has been developed a method of studying evolutionary trends in the secondary xylem of the dicotyledons, the fundamentals of which were laid principally by the researches of Bailey and Tupper *(13)*, Frost *(50, 51, 52)*, and Kribs *(64, 65)*.

The technique depends on the previous establishment of an undoubtedly primitive anatomical feature and this is then associated with the feature to be investigated in order to determine the extent and direction of the correlation between the occurrence of both features in the various species. A high positive correlation would indicate that the feature studied is relatively primitive. If a similar characteristic shows a more negative correlation with the established primitive feature, it would be considered more advanced and the line of specialization could then be read from the first to the second characteristic.

Frost applied this method in a study of the development of the vessel, using as his original primitive character the length of the tracheary elements. Bailey and Tupper had already shown that the most advanced element was the shortest one. Frost associated the length of the vessel with the type of perforation and the end wall and found a high degree of correlation between the primitive condition of length and the scalariform perforation. From data such as these and further detailed studies, he concluded that the vessel was derived from the scalariform tracheid and that the wood of the homoxylous angiosperms was very primitive.

These same methods were used by Kribs in studying the salient lines of specialization in the wood rays and wood parenchyma of dicotyledons. Using as the basis the vessel types of Frost, he came to the conclusion that the specialized types are the homogeneous rays and the vasicentric distribution of wood parenchyma.

Extensive investigations, such as those made by the above authors, on a wide range of representative dicotyledons have demonstrated statistically that the structural specialization of the

cambium and its derivatives tend in general to progress along a number of clearly defined lines. These salient lines of phylogenetic modification of the cambium and of the secondary xylem are not only more or less closely correlated, but also at times they synchronize with morphological specializations of the floral organs. Their significance in discussing the relationships and classification of families within certain orders of the dicotyledons has been shown by McLaughlin *(69)*, Tippo *(94)*, Vestal *(98)*, and others.

Extensive exploratory investigations have now progressed to a point where it has become desirable to initiate intensive studies of specific families. This is essential in obtaining more detailed information regarding the relative rates of specialization in different organs and tissues, and in securing clues regarding the actual significance of anatomical criteria in discussions concerning specific, generic, and tribal relationships.

The fundamental problems involved in this investigation have to do with the unity and distinctiveness of the groups which have been established within the family Tiliaceae. In other words, this study is concerned with the possibility of supporting one or more of the general conceptions as to the internal classification of the family based upon conclusions drawn from a detailed study of the secondary xylem. The attempt is made to use these anatomical data in tracing the relationships of the tribes and genera included within the family. Further, there has been an endeavor to harmonize the anatomical data with the facts of floral morphology.

ANATOMICAL INDICATORS OF PHYLOGENY

The anatomists have established, independently of taxonomy and systems of phylogeny, certain lines of specialization or trends of evolution in the structure of the plant stele. It is held by many anatomists *(48, 54, 55, 56, 62, 63, 68, 69, 78, 91, 94, 95, 100, 106)* that these evolutionary tendencies in the internal structure of the plant should be of some aid to taxonomy and to phylogeny. It must be made clear, however, that the anatomist is not striving to base classification on anatomical features alone. He does not argue that the anatomy of plants is necessarily more conservative than the structure of the flower or fruit. He recognizes that in evolution not all the structures of an organism may be proceeding in specialization at the same rate; thus, in some groups the flower probably has evolved relatively rapidly, while internal structures remain more or less at the same evolutionary level, while in

other groups the stem became more specialized with the reproductive organs remaining more or less the same. The anatomists do feel that any truly natural system of classification must take cognizance of the facts of internal structure as well as those of external morphology.

These lines of structural evolution, chiefly in the secondary xylem, may be summarized briefly as follows:

1. Diffuse-porous woods precede ring-porous woods *(50, 57)*.

2. The solitary arrangement of pores is more primitive than the various aggregate arrangements of pores; that is, pore multiples, pore clusters, and pore chains (*94* after Frost).

3. Primitive vessel members are characterized by thin, evenly thickened walls, and angular cross-sectional outline *(50)*.

4. The scalariform perforation is primitive and the porous perforation is specialized. The phylogenetic order of development is: scalariform, scalariform-porous, oblique-porous with vestiges of the scalariform condition, and transverse porous *(13, 19, 50, 51, 59, 92, 93)*.

5. Specialization of the scalariform perforation results in a widening of the perforation. The type with many bars (over 15) to a plate is primitive; the intermediate (5 to 15) bars comes next; and the type with few (5 or less) bars is highest *(51)*.

6. In the scalariform types the end wall is highly inclined or absent. The inclination of the end wall changes from the highly inclined position to a transverse position as the scalariform perforation develops into the porous perforation *(13, 50, 51)*.

7. The primitive fully bordered aperture of a scalariform perforation gradually loses its borders as the perforation becomes specialized *(51)*.

8. The lateral pitting of a vessel member specializes more rapidly than the specialization of the perforation *(51)*.

9. Scalariform intervascular pitting is primitive in the organization of the vessel members of the dicotyledons. Evidence indicates that vessel members with scalariform pitting on both the end and side walls are more primitive than vessel members with scalariform pitting on the end walls and opposite to alternate pitting on the side walls. Specialization of the scalariform pit produces transitional and opposite pitting. The rearrangement of opposite pits gives rise to the highly specialized alternate type of intervascular pits *(10, 13, 20, 41, 43, 50, 52)*.

10. Vessel-parenchyma pit-pairs may be scalariform, transitional, opposite, or alternate. The evolutionary sequence is the same as in the development of the intervascular *(49)*.

11. Vessel-parenchyma pit-pairs may be fully bordered, half-bordered, or nonbordered. The fully bordered pit-pair appears to be primitive and to give rise during specialization to the half-bordered and the simple type *(13, 20, 49, 50, 52)*.

12. The introduction of tertiary spirals in secondary vessel members is an evidence of specialization *(52)*.

13. There is a high correlation between vessel type and wood parenchyma type: the evolutionary sequence being from the diffuse parenchyma type, the most primitive, through the transitional diffuse-aggregate, vasicentric-scanty, and metatracheal types, to the highly specialized vasicentric abundant types. An absence of parenchyma indicates a primitive condition. Terminal parenchyma is a specialization due to reduction *(59, 65)*.

14. As woods become more highly specialized, the individual parenchyma cells parallel the development of the vessel elements in that they become shorter and wider *(65)*.

15. There is a phylogenetic decrease in length of the fibrous tracheary elements as the tracheids, fiber-tracheids, and libriform wood fibers become more specialized *(4, 13)*. The nonseptate fiber, either fiber-tracheid or libriform wood fiber, precedes the septate fiber-tracheids or septate libriform wood fibers *(94)*.

16. Heterogeneous wood rays are more primitive than homogeneous rays. Kribs has shown that the evolutionary sequence is from the heterogeneous type I, the most primitive, through the transitional heterogeneous type II A and II B, to the homogeneous type I, to the highly specialized homogeneous type II rays. Further, the uniseriate homogeneous type III rays are more highly specialized than the uniseriate heterogeneous type III rays. Heterogeneous type III is regarded as a derivative of either type I or II. Homogeneous type III may have evolved from any of the other types. It appears that the uniseriate types are highly specialized structurally owing to the elimination of the multiseriate rays *(64)*. The absence of rays is a highly specialized condition, associated with reduction of cambial activity and in many cases with a tendency toward the herbaceous habit of growth *(16)*.

17. Bailey *(5)* has shown that in structurally primitive woods, the fusiform initials of the cambium overlap and the increase in the circumference of the lateral meristem is due to pseudotransverse, anticlinal divisions followed by longitudinal sliding growth of these cells. Consequently the cells of the mature wood are nonstratified. This type of cambial activity culminates in a type where the anticlinal divisions of the fusiform initials are radio-longitudinal. In such stems the cambial derivatives are ar-

ranged in parallel horizontal series. Thus the storied arrangement, i.e., rays, vessel members, and even wood fibers and wood parenchyma strands, indicates a highly specialized stem *(76)*.

18. It appears that the abundance of sheath-cells and the method of enlarging the rays at the expense of the fusiform initials is a primitive feature, and that small-rayed species are on the whole more advanced than the large-rayed ones *(31)*.

TAXONOMIC HISTORY

The composition of the Tiliaceae has undergone many changes since the original designation of the group by Bernardi de Jussieu in 1759. His group, the Tiliae, consisted of 11 genera, five of which have remained in this family up to the present time, the remaining genera having been distributed among four families by later taxonomists. It is interesting to note that *Liriodendron* and *Magnolia* were included within this family by Jussieu.

The first attempt to subdivide the family came with Antonii de Jussieu *(60)* in 1789. Under his system the family consisted of three groups as follows: Tiliaceae Dubiae, Tiliaceae Verae, and the Tiliaceis Affinia. The three groups were separated on the basis of the stamens and the fruit, and the family consisted of a heterogeneous mixture of four or five present day families. This arrangement retained its prominence until 1824 when De Candolle *(23)* revised the family, retaining only the members of the Tiliaceae Verae of Jussieu.

The first important classification of the family was made by Endlicher *(43)* in his "Genera Plantarum." Under his system the family was subdivided into two suborders and four tribes as follows:

Suborder I. TILIACEAE VERAE

Corolla none or the petals entire; anthers opening longitudinally.

Tribe 1. Sloaneae. Corolla none.

1. *Hasseltia*
2. *Ablania*
3. *Dasynema*
4. *Sloanea*

Tribe 2. Grewieae. Corolla entire.

5. *Apeiba*
6. *Luhea*
7. *Mollia*
8. *Heliocarpus*
9. *Entelea*
10. *Sparmannia*
11. *Clappertonia*
12. *Corchorus*
13. *Corchoropsis*
14. *Triumfetta*
15. *Tilia*
16. *Brownlowia*
17. *Christiania*
18. *Grewia*
19. *Belotia*
20. *Diplophractum*
21. *Columbia*
22. *Berrya*
23. *Muntingia*
24. *Trilix*

Suborder II. ELAEOCARPEAE

Petals lacerate; anthers opening by a transverse valve at apex.

Tribe 3. Elaeocarpeae verae. Fruit drupaceous.

27. *Elaeocarpus*
28. *Monocera*
29. *Beythea*

Dubious genera
30. *Friesia*
31. *Acronodia*

Tribe 4. Tricuspidarieae. Fruit capsular or baccate.

32. *Vallea*
33. *Tricuspidaria*
34. *Crinodendron*

The classical revision of the family by Bentham and Hooker *(17)* in 1862 established the four tribes and their phylogenetic arrangement which has persisted to the present day with only minor revision. Under this system the Tiliaceae verae, with the exception of the Sloaneae of Endlicher, becomes the Series Holopetalae. From the tribe Grewieae of Endlicher are made three additional tribes, being separated on the basis of the calyx, corolla, and the anthers. The tribe Brownlowieae is placed in the primitive position on the basis of its three- to five-parted, partially united calyx. The remaining three tribes of this series are separated on the basis of petal insertion and the characters of the anthers; all three tribes possess a calyx consisting of distinct sepals. The tribe Apeibeae is placed in the highest position on the basis of its six- to many-chambered ovary.

Under the Bentham and Hooker system, the Suborder Elaeocarpeae of Endlicher becomes the Series Heteropetalae and includes Endlicher's tribe Sloaneae which he had placed in the Tiliaceae. The tribe Tricuspidarieae of Endlicher becomes the Elaeocarpeae and the additional tribe, the Prockieae, is founded.

The arrangement of the family as set up by Bentham and Hooker is outlined below.

SERIES A. HOLOPETALAE

Tribe I. Brownlowieae

1. *Brownlowia*
2. *Pentace*
3. *Diplodiscus*
4. *Pityranthe*
5. *Christiania*
6. *Berrya*
7. *Carpodiptera*

Tribe II. Grewieae

8. *Grewia*
9. *Desplatzia*
10. *Duboscia*
11. *Columbia*
12. *Diplophractum*
13. *Belotia*
14. *Erinocarpus*
15. *Triumfetta*
16. *Heliocarpus*

Tribe III. Tilieae

17. *Entelea*
18. *Sparmannia*
19. *Nettoa*
20. *Honckenya*
21. *Corchorus*
22. *Corchoropsis*

Tribe III. Tilieae (Continued)

23. *Luhea*
24. *Mollia*
25. *Trichospermum*
26. *Graffea*
27. *Muntingia*
28. *Tilia*
29. *Leptonychia*
30. *Schoutenia*

Tribe IV. Apeibeae

31. *Glyphaea*
32. *Apeiba*
33. *Ancistrocarpus*

SERIES B. HETEROPETALAE

Tribe V. Prockieae

34. *Prockia*
35. *Hasseltia*
36. *Plagiopteron*
37. *Ropalocarpus*

Tribe VI. Sloanieae

38. *Vallea*
39. *Sloanea*
40. *Echinocarpus*
41. *Antholoma*

Tribe VII. Elaeocarpeae

42. *Aristotelia*
43. *Elaeocarpus*
44. *Dubouzetia*
45. *Tricuspidaria*

Under the system of Engler and Prantl *(45)*, the Elaeocarpeae of Endlicher and the Series Heteropetalae of Bentham and Hooker became the family Elaeocarpaceae and was placed before the Tiliaceae. The family Elaeocarpaceae was reduced by seven genera and two tribes; the tribe Prockieae being entirely excluded. The tribes of the Tiliaceae were shifted somewhat in their phylogenetic position, the Brownlowieae remaining in the primitive position, while the Apeibeae was placed above the Brownlowieae. The Grewieae became the highest tribe of the family in contrast to its relatively low position under the arrangement of Bentham and Hooker. Thus, in 1895, the status of the two families was as follows:

Elaeocarpaceae

Tribe I. Elaeocarpeae

1. *Elaeocarpus*
2. *Sloanea*
3. *Crinodendron*
4. *Dubouzetia*
5. *Antholoma*

Tribe II. Aristotelieae

6. *Vallea*
7. *Aristotelia*

Tiliaceae

Tribe I. Brownlowieae

1. *Carpodiptera*
2. *Berrya*
3. *Christiania*
4. *Speirostyla*
5. *Oubanguia*
6. *Chartocalyx*
7. *Brownlowia*
8. *Pentace*
9. *Diplodiscus*
10. *Pityranthe*

Tribe II. Apeibeae

11. *Ancistrocarpus*
12. *Glyphaea*
13. *Apeiba*

Tribe III. Tilieae

14. *Nettoa*
15. *Entelea*
16. *Corchorus*
17. *Ceratosepalum*
18. *Corchoropsis*
19. *Cistanthera*
20. *Sparmannia*
21. *Honckenya*
22. *Luehea*
23. *Mollia*
24. *Graffea*
25. *Trichospermum*
26. *Schoutenia*
27. *Tilia*
28. *Vasivaea*

Tribe IV. Grewieae

29. *Grewia*
30. *Duboscia*
31. *Diplanthemum*
32. *Desplatzia*
33. *Grewiella*
34. *Diplophractum*
35. *Columbia*
36. *Belotia*
37. *Erinocarpus*
38. *Triumfetta*
39. *Heliocarpus*
40. *Pentadiplandra*
41. *Althoffia*

The systematic arrangement of Engler and Prantl has been generally accepted by the greater majority of taxonomists in regard to the separation of the two families. The partial monograph of the Tiliaceae made by Burret *(22)* in 1926 is entirely different from all the previous systems in its arrangement of the various tribes. Burret proposes three subfamilies and 16 tribes arranged as follows:

Brownlowioideae

I. Berryeae
1. *Berrya*
2. *Carpodiptera*

II. Christianieae
3. *Asterophorum*
4. *Tahitia*
5. *Christiania*

III. Brownlowieae
6. *Brownlowia*
7. *Diplodiscus*

IV. Pentaceae
8. *Pityranthe*
9. *Pentace*

Tetralicioideae

V. Tetraliceae
10. *Tetralix*
11. *Vasivaea*

Tilioideae

VI. Tilieae
12. *Tilia*
13. *Schoutenia*
14. *Sicrea*

VII. Grewieae
15. *Eleutherostylis*
16. *Grewia*
17. *Vinticena*
18. *Microcos*

VIII. Coloneae
19. *Colona*
20. *Goethalsia*

IX. Duboscieae
21. *Duboscia*
22. *Desplatsia*

X. Lueheeae
23. *Luehea*
24. *Luehopsis*
25. *Mollia*

XI. Trichospermae
26. *Trichospermum*
27. *Belotia*
28. *Althoffia*

XII. Triumfetteae
29. *Erinocarpus*
30. *Triumfetta*
31. *Heliocarpus*

XIII. Sparmannieae
32. *Honckenya*
33. *Sparmannia*
34. *Entelea*

XIV. Corchoreae
35. *Corchorus*

XV. Apeibeae
36. *Glyphaea*
37. *Ancistrocarpus*
38. *Apeiba*

XVI. Neotessmannieae
39. *Neotessmannia*

Edlin *(44)*, in his study of the various families included within the Malvales order, suggests the reinstatement of the Elaeocarpaceae under the Tiliaceae and placing it before the tribes of the Tiliaceae. The tribe Prockieae is restored to the Elaeocarpaceae and the group consists of 14 genera, some of which are genera which had been reduced to synonymy. The tribes of the Tiliaceae as instituted by Bentham and Hooker are retained but many synonymous genera have been restored. Thus, under Edlin's revision, which he made in 1935, the Tiliaceae is composed of 59 genera.

The arrangement of the Tiliaceae-Elaeocarpaceae complex as suggested by Edlin is outlined below.

TILIACEAE

I. Elaeocarpeae
1. *Elaeocarpus*
2. *Sloanea*
3. *Crinodendron*
4. *Dubouzetia*
5. *Antholoma*
6. *Muntingia*
7. *Anoniodes*
8. *Sericolea*
9. *Aceratium*

II. Aristotelieae
10. *Vallea*
11. *Aristotelia*

III. Prockieae
12. *Prockia*
13. *Hasseltia*
14. *Plagiopteron*

IV. Brownlowieae
15. *Carpodiptera*
16. *Berrya*
17. *Christiana*
18. *Chartocalyx*
19. *Brownlowia*
20. *Pentace*
21. *Diplodiscus*
22. *Pityranthe*
23. *Asterophorum*
24. *Tahitia*

V. Apeibeae
25. *Ancistrocarpus*
26. *Glyphaea*
27. *Apeiba*

VI. Tilieae
28. *Entelea*
29. *Corchorus*
30. *Sparmannia*
31. *Honckenya*
32. *Luehea*
33. *Mollia*
34. *Graeffea*
35. *Trichospermum*
36. *Schoutenia*
37. *Tilia*
38. *Vasivaea*
39. *Luehopsis*
40. *Ceratosepalum*
41. *Cephalonema*
42. *Tetralix*
43. *Sicrea*

VII. Grewieae

44. *Grewia*
45. *Duboscia*
46. *Desplatzia*
47. *Diplophractum*
48. *Columbia*
49. *Belotia*
50. *Erinocarpus*
51. *Heliocarpus*
52. *Althoffia*
53. *Ledermannia*
54. *Goethalsia*
55. *Cotylonychia*
56. *Eleutherostylis*
57. *Grewiopsis*
58. *Halconia*
59. *Triumfetta*

MATERIALS AND METHODS

The present investigation was based on the study of 578 specimens representing 206 species and 37 genera. Small blocks of the wood were boiled, cooled, and then softened in hydrofluoric acid. The material was washed and then stored in glycerin-alcohol. Later transverse, radial, and tangential sections were cut with a Spencer sliding microtome. These sections, 10 to 15 μ in thickness, were stained in Delafield's haematoxylin and then counterstained in safranin. A small portion of each specimen was macerated with Jeffrey's maceration solution and the material then mounted in glycerin-jelly.

The terms used in the anatomical descriptions of the genera which follow this section are those approved by the Committee on Nomenclature of the International Association of Wood Anatomists *(34)*. These terms have been further elaborated and illustrated by Record, the chairman of the committee *(79)*.

Krib's classification of rays is used in this investigation. Ray width and ray height do not appear to have much phylogenetic significance except in possibly a few cases; indeed it is questionable whether they are of any great diagnostic value for they exhibit considerable variation, not only from tree to tree, but at different levels in the same tree, and at various distances from the pith at the same level *(3, 15, 38, 71, 102)*.

However, a brief notation on the range of variation in ray width and height is included in the anatomical description of each genus. Krib's classification is given here so that needless repetition of ray description will thus be eliminated in the generic descriptions.

Heterogeneous. Type I.

Uniseriate rays usually high, numerous, and composed of very large, vertically elongated cells which are unlike the cells of the multiseriate part of the multiseriate rays.

Multiseriate rays usually with parallel sides and with very large, vertically elongated, uniseriate wings which are composed of cells identical with those of the uniseriate rays. The cells of

the multiseriate portion of the rays are oval, radially elongated, or vertically elongated.

Heterogeneous. Type II.

A. Uniseriate rays composed of rectangular, vertically elongated cells only.

Multiseriate rays with sides parallel or fusiform, the cells of the multiseriate portion being round or oval, usually radially elongated, and with uniseriate tips of large, vertically elongated cells; or with large vertically elongated marginals, one cell high.

B. Uniseriate rays of two types: some of the uniseriate rays composed of rectangular, vertically elongated cells; some composed of cells which are nearly identical with those of the multiseriate parts of the multiseriate rays.

Multiseriate rays with sides parallel or fusiform, the cells of the multiseriate portion being round to oval, radially elongated, and with medium to small, vertically elongated marginals, usually single, occasionally two cells high. If the uniseriate tips are longer the cells are modified; that is, they are mostly square.

Homogeneous. Type I.

Uniseriate rays rather low, numerous to scarce, and composed of cells which are identical with those of the multiseriate rays.

Multiseriate rays mostly fusiform, the cells of the multiseriate portions being round to oval, radially elongated, and with long to short, uniseriate tips composed of cells identical with those of the multiseriate portion of the ray. Occasionally a multiseriate ray possesses very small square marginals, one cell high, which occur sporadically.

Homogeneous. Type II.

Uniseriate rays usually scarce to absent; when present, low, and composed of cells identical with those of the multiseriate rays.

Multiseriate rays fusiform; composed entirely of small, round, radially elongated cells; uniseriate tips present or very short.

Whenever the anatomical description of a genus was, by necessity, based on material cut from a region close to the pith, this fact is indicated. The ideal situation, of course, would be one where it would be possible always to compare the homologous parts of the plants of all the genera, for it has been shown *(7)* that in a given species the range of variability tends to be greater in different parts of a single, large mature tree than in homologous parts of different trees. Since this ideal arrangement is not always possible to attain, the next best thing is to record any youthful material employed in an investigation so that a correction may be made in the interpretation of any conclusions based

on this young material. Many investigators *(12, 13, 24, 61, 75, 90)* have shown that from the pith outward, the lengths of vessel elements and other tracheary cells increase very rapidly for a number of years, and then remain at about the same relative length, but fluctuating slightly with changes in environmental conditions. Vessel diameter also increases from the pith out to the bark *(4, 75)*. Multiseriate ray width increases centrifugally from the pith *(38)*. Multiseriate ray depth seems to decrease from the pith outward *(15)*.

Further, plants with homogeneous rays in the mature wood may have heterogeneous rays in the wood near the pith. Thus it seems that there is an increase in the homogeneity of the rays from the pith out to the cambium. Enough has been said about the variation from youth to old age in wood to demonstrate the importance of using homologous regions in comparative anatomical studies. At least, if this is not always possible, any departure from the use of homologous material should be recorded.

MEASUREMENTS

Vessel Members

Vessel members were measured from slides of macerated material with a graduated ocular disc calibrated against a stage micrometer. Total body length (that is, the extreme tip of one end to the tip of the other) was measured, since it has been shown that total body length, rather than body length or extreme body length, corresponds more nearly to the length of the cambial initial from which the vessel member was derived *(26)*. From each specimen, 100 vessel members were measured and the standard deviation and standard errors calculated for each genus and recorded in the generic descriptions. The standard errors obtained were in all cases considerably below the recommended 10 per cent limit of variation. The size classes recorded for vessel member length are those recommended by the Committee on Standardization of Terms of Cell Size of the International Association of Wood Anatomists *(35)*, and are defined as follows:

Short	
Extremely short	Less than 175 μ
Very short	175 to 250 μ
Moderately short	250 to 350 μ
Medium-sized	
Medium-sized	350 to 800 μ
Long	
Moderately long	800 to 1,100 μ
Very long	1,100 to 1,900 μ
Extremely long	over 1,900 μ

Pore Diameter

Although both the radial and the tangential diameters of pores are frequently used in descriptions, it is probable that one is actually sufficient. The tangential diameter is preferable, as it is less variable and the approximate radial diameter can be inferred when the shape of the pore is given in the description. Pore diameters were measured from cross section and 25 to 100 measurements were made on each specimen depending on the number of samples which were available for the genus under consideration. In making the measurements, only solitary pores and the largest members of pore multiples were considered. The standard deviation and standard error were calculated for each genus and are recorded in the descriptions.

Numerical Distribution of Pores

The number of pores in a given area of the cross section is a useful indication of the texture and general character of the wood and is usually included in systematic descriptions. This method is applicable only to timbers with a fairly even distribution of pores and pore groups.

The number of pores per square millimeter was measured by the projection method (that is, the scale of a stage micrometer was projected on white cardboard and an area of one square millimeter outlined). The values obtained were derived from 10 measurements on each sample within a genus and were made in radial strips so that as many growth rings as possible would be included. The range and the mean are recorded for each genus. Radial multiples and clusters are regarded as single pores in making the counts.

Pore Grouping

The pores of this family occur singly or in short radial multiples of 2 to 4, and less frequently in clusters of 3 to 6 pores. The percentages recorded in the descriptions were obtained by making counts of the different pore types which occurred in a strip across the cross section extending in the radial direction so as to include as many growth rings as possible.

Pore Wall Thickness

This measurement was made on the radial walls and only 10 observations were made on each sample. The radial wall thickness was selected since it exhibits less variation than the tangential wall thickness; tangential walls in contact with adjacent

pores are always thicker than the radial walls and exhibit considerable variation. Measurements were made on the cross section.

Fiber Length

Fiber length was measured from slides of macerated material and 50 measurements were made on each specimen. The standard deviation and standard error are recorded for each genus; the standard error in all cases is well under the 10 per cent limit. The size classes used are those as recommended *(35)*, and are defined as follows:

Short	
Extremely short	Less than 500 μ
Very short	500 to 700 μ
Moderately short	700 to 900 μ
Medium-sized	
Medium-sized	900 to 1,600 μ
Long	
Moderately long	1,600 to 2,200 μ
Very long	2,200 to 3,000 μ
Extremely long	over 3,000 μ

Fiber Diameter

Fiber diameter values were obtained from 10 measurements on each sample. The values in themselves have no particular value but are used merely to complete the description. The same procedure was used in obtaining the average fiber wall thickness.

Parenchyma Width and Length

The values recorded for wood parenchyma width (tangential) and length were obtained by measuring 10 cells on each sample within the genus. The width of the cells was measured from cross sections and the length from radial sections.

DESCRIPTION OF THE WOODS OF THE TILIACEAE

Pentace Hassk. (1858)

Genus of 12 species distributed in the Philippine Islands, East Indies, Burma, and India. Description based on 38 specimens representing 10 species.

Growth rings indistinct or lacking to distinct and delimited by uniseriate or biseriate bands of terminal parenchyma; sometimes defined only by bands of thicker-walled, radially flattened wood fibers. Wood rays spreading at limits of growth rings.

Pores generally oval on cross section; 3 to 13 per square mm., average 7; tangential diameter range from 75 to 234 μ, average 149 μ (S.E. 2.23 μ, S.D. 29 μ); pore walls average 3.5 μ

in thickness. Pores mostly solitary (51 per cent) and in radial multiples of 2 to 4 (45 per cent), the remaining in radial multiples of 5 to 8 and in tangential pairs or clusters of 3 to 7 pores; distributed without pattern.

Vessel members very short to medium-sized, average 449 μ in length (S.E. 2.25 μ, S.D. 69 μ); perforation plates simple, transverse to obliquely inclined. Gum deposits few to abundant.

Intervessel pit-pairs 1.5 to 3 μ in diameter; alternate; round or oval, with oval, included apertures.

Vessel-ray pit-pairs half-bordered; unilaterally compound, a single ray pit subtending 2 to 12 vessel pits, elongated vertically or horizontally and up to 20 μ in length; sometimes merely elongated and not subtending any vessel pits.

Vessel-parenchyma pit-pairs half-bordered; unilaterally compound or like above, a parenchyma pit subtending 2 to 15 vessel pits; generally elongated horizontally and up to 18 μ in length.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The terminal, when present, uniseriate to biseriate. The paratracheal parenchyma commonly forming a complete uniseriate sheath about the pores; generally more abundant in the late wood of the growth rings. Reticulate parenchyma disposed in concentric tangential lines which are mostly uniseriate or up to 3 seriate in the vicinity of the terminal parenchyma; the bands continuous across the wood rays and about 5 fiber rows apart. Diffuse parenchyma consists of isolated cells or short irregular lines between the bands of zonate parenchyma. Parenchyma cells average 27 μ in tangential width and 121 μ in length; generally without contents.

Wood rays heterogeneous II B to homogeneous I; 5 to 9 per mm., average 7. Rays regularly storied; mostly 2 to 4, sometimes up to 5, seriate. Normal multiseriate rays (those which do not appear to be vertically fused) average 353 μ in height and are never over 68 μ in width. Vertically fused rays infrequent, when present generally are two to three times the height of the normal rays. Ray cells on radial section mostly tabular, the marginals erect or only slightly higher than the body cells. Uniseriate rays sparse or lacking.

Wood fibers medium-sized to very long, average 1,649 μ in length (S.E. 10 μ, S.D. 230 μ); average middle diameter of 25 μ and wall thickness of 3 μ. Fibers generally long-tapering; infrequently bifurcate. Pits bordered; mostly 3 to 5 μ in diameter; oval, with included apertures which are oval or with slitlike, extended apertures.

Diplodiscus Turcz. (1858)

Genus of three species distributed in the Philippine and Sulu Islands. Description based on 25 specimens representing two species.

Growth rings present; delimited by bands of terminal parenchyma which are 1 to 3 seriate and generally interspersed with wood fibers. Wood rays spreading at the limits of the growth rings.

Pores generally oval; 4 to 12 per square mm., average 8; tangential diameter range from 45 to 211 μ (S.E. 0.93 μ, S.D. 25 μ); pore walls average 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (52 per cent) and solitary (32 per cent), the remaining in radial multiples of 5 to 7 and in tangential pairs or clusters of 3 to 8 pores; distributed without pattern.

Vessel members very short to medium-sized, average 378 μ in length (S.E. 2.33 μ, S.D. 58 μ); perforation plates simple, transverse to slightly inclined. Tyloses present; pitted; walls up to 2 μ in thickness.

Intervessel pit-pairs 1.5 to 2.5 μ in diameter; round or oval, with included, lenticular apertures; alternately arranged.

Vessel-ray pit-pairs half-bordered; unilaterally compound; elongated vertically and up to 30 μ in length.

Vessel-parenchyma pit-pairs half-bordered; unilaterally compound and in the shape of a flattened oval or oval to round; generally elongated both horizontally and vertically and attain a length of 32 μ.

Wood parenchyma terminal, paratracheal, and reticulate. The terminal forming interrupted bands which are 1 to 3 seriate at the limits of the growth rings. Reticulate parenchyma abundant; forming tangential lines 2 to 5 cells in length between the wood rays and commonly 3 fiber rows apart. Paratracheal parenchyma usually forming a complete uniseriate sheath about the pores. Parenchyma cells average 25 μ in tangential width and 87 μ in length. Yellow-brown deposits and crystals common.

Wood rays heterogeneous II B to homogeneous I; 7 to 14 per mm., average 10. Multiseriate rays 2 to 8, mostly 3 to 5, seriate; those regularly storied average 350 μ in height and 23 to 38 μ in width. Vertically fused rays few to common; range in height from 600 to a maximum of 2,378 μ. Ray cells mostly radially elongated, the marginals erect. Yellow-brown contents and crystals common.

Wood fibers very short to very long, average 1,654 μ in length (S.E. 14 μ, S.D. 320 μ); average middle diameter of 21 μ and wall

thickness of 5 μ. Fibers long-tapering. Pits bordered; radially flattened and 3 to 5 μ in diameter; apertures slitlike, included or extended.

Brownlowia Roxb. (1819)

Humea Roxb.; *Braunlowia* DC; *Dialycarpa* Mast.

Genus of 17 species distributed in the Philippine Islands, East Indies, Indo-China, Burma, and India. Description based on two specimens representing two species.

Growth rings present; delimited by interrupted, uniseriate to biseriate bands of terminal parenchyma. Rays spreading at limits of growth rings.

Pores generally oval in outline; 6 to 9 per square mm., average 8; tangential diameter range from 81 to 151 μ, average 118 μ (S.E. 2.39 μ, S.D. 17 μ); pore walls 2 to 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (56 per cent) and solitary (41 per cent), the remaining in tangential pairs or in clusters of 3 to 6 pores; distributed without pattern.

Vessel members very short to medium-sized, average 375 μ in length (S.E. 5.78 μ, S.D. 58 μ); perforation plates simple, transverse to slightly inclined.

Intervessel pit-pairs round or oval; 3 μ in diameter; alternate; with included, lenticular apertures.

Vessel-ray pit-pairs half-bordered; unilaterally compound; the ray pit subtending 5 to 8 vessel pits; flattened oval or irregular in shape and up to 25 μ in length; mostly horizontal.

Vessel-parenchyma pit-pairs half-bordered; unilaterally compound; elongated both horizontally and vertically and up to 17 μ in length.

Wood parenchyma terminal, reticulate, and paratracheal. The terminal consisting of interrupted, uniseriate to biseriate bands at the limits of the growth layers. Reticulate parenchyma abundant, mostly in uniseriate tangential to oblique lines of 3 to 10, mostly 3 to 5, cells between the wood rays or sometimes continuous across the rays. Paratracheal parenchyma generally forming a complete uniseriate sheath about the pores. Parenchyma cells average 28 μ in tangential diameter and 87 μ in length. Brown deposits common.

Wood rays heterogeneous II B; 7 to 10 per mm., average 8. Multiseriate rays 3 to 8, mostly 4 to 6, seriate; quite variable in height; mostly about 750 μ in height with a maximum of 1,360 μ; the rays 38 to 90 μ in width, average 60 μ. Cells on radial section mostly radially elongated, the marginals erect or square. Brown

deposits common; crystals present. Uniseriate rays average 250 μ in height. All rays storied; the high rays in secondary seriation.

Wood fibers medium-sized to very long, average 1,904 μ in length (S.E. 32 μ, S.D. 230 μ); middle diameter average of 18 μ and walls 3 to 5 μ in thickness. Fibers long-tapering, the ends frequently bent or serrated. Pits bordered; the apertures slitlike, long-extended.

Berrya Roxb. (1814)

Espera Willd.; *Hexagonotheca* Turcz.; *Pterocoellion* Turcz.

Genus of three species distributed in India, Ceylon, the Philippines, Andaman and Nicobar Islands, Burma, Indo-China, and Java. Description based on 11 specimens representing 2 species.

Growth rings distinct; delimited by uniseriate bands of terminal parenchyma or of isolated parenchyma cells interspersed with flattened wood fibers. Rays spreading.

Pores round or oval; 6 to 14 per square mm., average 10; tangential diameter range from 30 to 181 μ, average 113 μ (S.E. 1.34 μ, S.D. 30 μ); pore walls mostly 3 to 5 μ in thickness. Pores mostly in radial multiples of 2 to 4 (50 per cent) and solitary (41 per cent), the remaining in radial multiples of 5 to 7 and in clusters of 3 to 6 pores; distributed without pattern.

Vessel members very short to medium-sized, average 334 μ in length (S.E. 1.23 μ, S.D. 39 μ); perforation plates simple, transverse to slightly inclined. Tyloses abundant; thin-walled, pitted.

Intervessel pit-pairs half-bordered; round or oval to slightly polygonal; commonly 3 μ in diameter; with lenticular, included apertures.

Vessel-ray pit-pairs half-bordered; unilaterally compound or elongated and subtending no vessel pits; variable in form but generally in the form of a flattened oval, elongated vertically.

Vessel-parenchyma pit-pairs like the vessel-ray pit-pairs but the unilaterally compound pitting is not so conspicuous because it is much smaller in size. Unilaterally compound pitting accompanied by normal pitting round or oval and about the size of the intervessel pitting.

Parenchyma terminal, paratracheal, paratracheal-banded, and diffuse. The terminal forming interrupted uniseriate bands at the limits of the growth rings. Paratracheal parenchyma sparse to abundant. Paratracheal-banded parenchyma 1 to 9 seriate in irregular short to long, concentric, tangential bands or arcs. Diffuse parenchyma occurring as single isolated cells or small clusters between the wood rays and the bands of zonate parenchyma.

Wood rays heterogeneous II B to homogeneous I; 7 to 11 per mm., average 8. Multiseriate rays 1 to 6, mostly 3 to 5, seriate; average 274 μ in height and 40 μ in width; vertically fused rays generally twice the height given above, sometimes reaching a height of 1,975 μ. Uniseriate rays few to common. Rays regularly storied; the fused rays in secondary seriation. Dark brown contents common; crystals abundant.

Wood fibers very short to very long, average 1,739 μ in length (S.E. 16 μ, S.D. 370 μ); middle diameter average of 20 μ and with a wall thickness of 2 to 10, mostly 3 to 7, μ. Fiber long-tapering, frequently with serrated tips. Pits bordered; 1 to 3 μ in diameter; with oval included apertures or slitlike, extended apertures.

Christiania (Christiana) DC. (1824)

Christiannia Walp.; *Speirostyla* Baker.

Two species. One in Madagascar; one distributed from Central Africa to the Cameroons and Senegambia to Northern Brazil, British Guiana, and British Honduras. Description based on eight specimens representing one species.

Growth rings present; delimited by continuous bands of 1 to 3 seriate terminal parenchyma or sometimes only by flattened wood fibers and isolated lines of terminal parenchyma. Wood rays spreading.

Pores round to slightly oval; 6 to 13 per square mm., average 8; tangential diameter range from 60 to 103 μ, average 92 μ (S.E. 2.96 μ, S.D. 14 μ); pore walls average 3.5 μ in thickness. Pores mostly in radial multiples of 2 to 4 (63 per cent) and solitary (34 per cent), the remaining in tangential pairs or clusters of 3 to 4 pores; distributed without pattern.

Vessel members moderately short to medium-sized; average 333 μ in length (S.E. 149 μ, S.D. 42 μ); perforation plates simple, transverse to slightly inclined. Tyloses present.

Intervessel pit-pairs round or oval to slightly polygonal; mostly about 5 μ in diameter; alternate; with flattened-oval, included apertures.

Vessel-ray pit-pairs half-bordered; normal to unilaterally compound; the normal, 3 to 7 μ in diameter and the unilaterally compound up to 20 μ in length; apertures flattened-oval or irregularly rounded.

Vessel-parenchyma pit-pairs half-bordered; normal to unilaterally compound; 5 to 15 μ in diameter or length.

Wood parenchyma terminal, paratracheal, paratracheal-banded, and diffuse. The terminal in irregular, 1 to 3 seriate, more

or less continuous, bands. Paratracheal parenchyma occurring sparsely about the pores which are isolated between the bands of zonate parenchyma. Paratracheal-banded parenchyma in short to long tangential lines which are mostly 2 to 4, up to 8, seriate and generally about 20 fiber rows apart. Diffuse parenchyma occurs in the vicinity of pores which are isolated between the zonate bands of parenchyma and at the ends of the zonate line of paratracheal-banded parenchyma. Parenchyma cells average 25 μ in tangential width and 92 μ in length; walls 1.5 μ in thickness.

Woods rays heterogeneous II B to homogeneous I; 16 to 19 per mm., average 17. Rays 1 to 5, mostly 2 to 3, seriate and regularly storied. Rays average 304 μ in height and 29 μ in width. On the radial section the cells are radially elongated, the marginals like the body cells or somewhat higher. Yellow-brown contents present.

Wood fibers medium-sized to very long, average 1,793 μ in length (S.E. 12 μ, S.D. 250 μ); middle diameter average of 20 μ and wall thickness of 8 μ. Fibers long-tapering, sharp-pointed. Pits round or oval; bordered; 1.5 to 3 μ in diameter; with included or only slightly extended, slitlike apertures.

Carpodiptera Griseb. (1861)

Genus of six species distributed in East Africa, Comoro Islands, Cuba, Haiti, St. Vincent, Grenada, and Trinidad. Description based on three specimens representing two species.

Growth rings present; delimited by bands of terminal parenchyma which are more or less continuous and irregularly 1 to 3 seriate. Rays spreading.

Pores round or slightly oval; 17 to 32 per square mm., average 24; tangential diameter range from 38 to 91 μ, average 66 μ (S.E. 2.48 μ, S.D. 18 μ); pore walls commonly 2 to 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (53 per cent) and solitary (44 per cent), the remaining in clusters of 3 to 4 pores; distributed without pattern.

Vessel members extremely short to medium-sized, average 271 μ in length (S.E. 2.18 μ, S.D. 38 μ); perforation plates simple, transverse to slightly inclined. Vessels without contents.

Intervessel pit-pairs round or oval; 3 μ in diameter; with lenticular apertures, the tips of which extend to the pit margins and frequently coalesce with adjacent pit apertures.

Vessel-ray pit-pairs half-bordered; normal and of the same size as the intervessel or unilaterally compound and up to 20 μ in length; the various forms generally occurring together.

Vessel-parenchyma pit-pairs like the vessel-ray pit-pairs or only slightly smaller.

Wood parenchyma terminal, paratracheal, paratracheal-banded, and diffuse. The terminal forming a more or less continuous, 1 to 3 seriate, band at the limits of the growth rings. Paratracheal parenchyma sparse, never completely enclosing the pores which are isolated between the bands of zonate parenchyma. Paratracheal-banded parenchyma abundant; irregularly 1 to 6 seriate and continuous across the wood rays, contacting the pores on one side only or sometimes engulfing the pores and pore groups; the bands generally 2 to 12 fiber rows apart. Diffuse parenchyma consisting of single cells often isolated between the zonate bands of parenchyma; sometimes occurring as short lines 1 to 4 cells long near the ends of the zonate bands or between them. Parenchyma cells average 19 μ in tangential width and 81 μ in length; the cell walls average 1.5 μ in thickness. Cells without contents.

Wood rays homogeneous I to heterogeneous II B; 8 to 11 per mm., average 9. Rays uniseriate and biseriate; the biseriate rays average 238 μ in height and 24 μ in width. Ray cells radially elongated with marginals like the body cells or square and slightly higher than the body cells. Uniseriate rays are of the same height as the biseriate. Rays regularly storied with the vessels and parenchyma strands. Light brown deposits common; crystals sparse.

Wood fibers medium-sized to moderately long, average 1,533 μ in length (S.E. 19 μ, S.D. 230 μ); middle diameter average of 15 μ and a wall thickness of 6 μ. Fibers long-tapering, sharp-pointed. Pits bordered; round or oval; 1.5 to 4 μ in diameter; with slitlike, slightly extended apertures.

Chartacalyx Maingay ex Mast. (1874)

Monotypic genus distributed in Java and Malaya. Description based on seven specimens.

Growth rings delimited by uniseriate or biseriate bands of flattened wood fibers interspersed with terminal parenchyma cells. Wood rays spreading at limits of growth rings.

Pores round or oval; 17 to 30 per square mm., average 23; tangential diameter range of 53 to 106 μ, average 74 μ (S.E. 1.71 μ, S.D. 12 μ); pore walls commonly 3 to 5 μ thick. Pores mostly in radial multiples of 2 to 4 (53 per cent) and solitary (43 per cent), the remaining in tangential pairs or clusters of 3 to 4 pores; distributed without pattern.

Vessel members extremely short to medium-sized, average 292 μ in length (S.E. 1.16 μ, S.D. 31 μ); perforation plates simple, transverse to somewhat oblique. Tertiary spirals present in the smaller vessels. Vessels without contents.

Intervessel pit-pairs round or oval; 1.5 to 2 μ in diameter; with oval, included apertures; alternate in arrangement.

Vessel-ray pit-pairs half-bordered; like the intervessel in shape but up to 3 μ in diameter. Vessel-parenchyma pit-pairs like the vessel-ray pit-pairs in shape and size.

Wood parenchyma terminal, paratracheal, and paratracheal-banded. The terminal parenchyma consisting of cells interspersed among the radially flattened wood fibers. Paratracheal parenchyma forming a uniseriate to biseriate sheath about the pores which occur between the bands of zonate parenchyma. Paratracheal-banded parenchyma in short tangential or oblique bands, 1 to 6, mostly 2 to 3, cells wide. Parenchyma cells average 20 μ in tangential width and 69 μ in length. The cells commonly with light brown contents.

Wood rays heterogeneous II B to homogeneous I; 9 to 11 per mm., average 10. The rays practically all 2 to 3, infrequently 4, seriate; mostly 23 to 30 μ, up to 45 μ in width and average 249 μ in height. The rays interspersed with large, square cells which either contain large crystals or appear empty. All elements storied.

Wood fibers moderately short to moderately long, average 1,547 μ in length (S.E. 11 μ, S.D. 212 μ); middle diameter average of 17 μ and average wall thickness of 7 μ. Fibers long-tapering, sharp-pointed. Pits bordered; oval; 3 μ in diameter; with included, slitlike apertures.

Schoutenia Korth. (1848)

Actinophora Wall.

Genus of five species distributed in Java, Borneo, Malaya, Indo-China, and Burma. Description based on eight specimens representing two species.

Growth rings delimited by bands of flattened wood fibers interspersed with terminal parenchyma cells. Wood rays spreading.

Pores round or oval; 3 to 6 per square mm., average 4; tangential diameter range from 60 to 166 μ, average 132 μ (S.E. 3.52 μ, S.D. 25 μ); pore walls average 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (54 per cent) and solitary (35 per cent), the remaining in tangential pairs or clusters of 3 to 8 pores; distributed without pattern.

Vessel members extremely short to medium-sized, average 394 μ in length (S.E. 1.99 μ, S.D. 56 μ); perforation plates simple, transverse to slightly oblique. Gum deposits present.

Intervessel pit-pairs round; 1.5 to 2 μ in diameter; with round, included apertures; alternate in arrangement.

Vessel-ray pit-pairs half-bordered; like the intervessel in shape but up to 3 μ in diameter; the vessel-parenchyma pit-pairs like the vessel-ray pit-pairs; both types alternate in arrangement.

Wood parenchyma terminal, paratracheal, and reticulate. The terminal parenchyma interspersed among the flattened wood fibers at the limits of the growth rings. Paratracheal parenchyma generally forming a uniseriate sheath about the pores when not interrupted by the wood rays. Reticulate parenchyma forming uniseriate tangential or oblique lines between the wood rays; the lines usually 2 to 3 fiber rows apart. The parenchyma cells average 16 μ in tangential width and 109 μ in length. The cells commonly with brownish-colored contents.

Wood rays heterogeneous II A; 13 to 18 per mm., average 15. Multiseriate rays normal and vertically fused; the normal rays average 853 μ in height and 45 μ in width; commonly 4 to 6 seriate. The multiseriate rays with large thick-walled cells interspersed among the small cells of the ray; practically all of these cells contain large crystals; on the radial section these cells form long radial lines which are very conspicuous and appear to form a constant feature for this genus. The body cells of the rays are tabular in shape and the marginals are square or erect. Brown contents common. Crystals apparently limited to the large cells. Rays not storied.

Wood fibers very short to moderately long, average 1,199 μ in length (S.E. 11 μ, S.D. 215 μ); average middle diameter of 18 μ and wall thickness of 3 μ. Fibers long-tapering, sharp-pointed. Pits bordered; oval; usually about 3 μ in diameter and with slit-like, included, or slightly extended apertures.

Tilia L. (1753)

Genus of 10 to 12 (20 to 30) species distributed throughout the greater part of the North Temperate Zone and Mexico. Description based on 109 specimens representing 29 species and varieties.

Growth rings distinct; delimited by bands of flattened wood fibers and terminal parenchyma. Wood rays spreading broadly at the limits of the growth layers.

Pores angular in cross-sectional outline; 24 to 112 per square mm., average 59; tangential diameter range from 23 to 106 μ,

average 63 μ (S.E. 0.43 μ, S.D. 11.5 μ); pore walls average 1.5 μ in diameter. Pores mostly solitary (56 per cent) and in radial multiples of 2 to 4 (31 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 2 to 7 pores; distributed without pattern but the pores become somewhat smaller in diameter from one end of the growth ring to the other.

Vessel members very short to medium-sized, average 461 μ in length (S.E. 1.73 μ, S.D. 91 μ); perforation plates simple, obliquely inclined. Tyloses few to abundant; thin-walled. All vessels with tertiary spirals.

Intervessel pit-pairs round or oval to polygonal; 3 to 8, mostly 3 to 5, μ in diameter; with lenticular, included apertures; alternate.

Vessel-ray pit-pairs and vessel-parenchyma pit-pairs identical; half-bordered; 3 to 5 μ in diameter; round or oval with lenticular, included apertures or with large apertures of the same shape as the pit outline; alternate.

Wood parenchyma terminal and reticulate. The terminal parenchyma generally forming a continuous uniseriate band or at times merely interspersed among the flattened wood fibers at the limits of the growth ring. The reticulate parenchyma forming uniseriate tangential or oblique lines between the wood rays; the individual cells either side by side or staggered. Yellowish-brown contents common. Parenchyma cells average 26 μ in tangential width and 95 μ in length.

Wood rays heterogeneous II B; 3 to 10 per mm., average 6. Multiseriate rays 3 to 4 seriate and commonly 23 to 38 μ in width; height extremely variable, ranging from 265 to 2,265 μ in height but mostly between 750 and 1,500 μ in height. The cells on radial section all tabular. The uniseriate rays generally very low and seldom exceed 300 μ in height. Yellowish-brown contents present; crystals sparse or lacking. Sheath cells extremely sparse; generally lacking in most specimens. Rays unstoried.

Wood fibers very short to moderately long, average 1,086 μ in length (S.E. 10 μ, S.D. 250 μ); middle diameter average of 26 μ and wall thickness of 2 to 2.5 μ. Fibers long to short-tapering; generally sharp-pointed. Pits bordered; round or oval; 5 to 7 μ in diameter; apertures—included, lenticular or slitlike, extended.

Grewia L. (1753)

Chadara Forsk.; *Grevia* L.; *Mallococca* Forst.; *Charadra* Scop.; *Graevia* Neck.; *Balmeda* Nocca.

Genus of about 90 species distributed in East Africa, Arabia, India, Burma, South China, Indo-China, East Indies, Philippines,

Northern Australia, South Pacific Islands to Fiji. Description based on 80 specimens representing 30 species.

Growth rings present; delimited by uniseriate to biseriate bands of terminal parenchyma; occasionally delimited by bands which are 1 to 5 seriate. Wood rays spreading at limits of growth rings.

Pores round to slightly oval; 2 to 51 per square mm., average 13; tangential diameter range from 30 to 204 μ, average 103 μ (S.E. 1.18 μ, S.D. 30 μ); pore wall thickness ranges from 2 to 8 μ. Pores mostly solitary (61 per cent) and in radial multiples of 2 to 4 (30 per cent), the remaining in radial multiples of 5 to 7 and tangential pairs or clusters of 3 to 9 pores; evenly distributed throughout growth ring.

Vessel members extremely short to medium-sized, average 259 μ in length (S.E. 1.38 μ, S.D. 54 μ); perforation plates simple, transverse to oblique. Gum deposits or tyloses few to abundant.

Intervessel pit-pairs round or oval to polygonal; 3 to 8, mostly 5 to 8, μ in diameter; with oval to lenticular, included apertures; the apertures frequently coalescing.

Vessel-ray pit-pairs half-bordered; 3 to 7 μ in diameter; round or oval, with oval or lenticular, included apertures. Vessel-parenchyma pit-pairs similar; sometimes smaller in size.

Parenchyma terminal, paratracheal, paratracheal-banded, reticulate, and diffuse. The terminal parenchyma forming bands 1 to 5, mostly 1 to 2, seriate at the limits of the growth rings. Paratracheal parenchyma generally forming a uniseriate sheath about the pores but in some species is very abundant and forms a sheath 2 to 3 seriate about the pores. Paratracheal-banded parenchyma occurring in some species but only in very short bands between adjacent pores. Reticulate parenchyma limited to a few species, where it occurs only in the late wood portion of the growth ring; consisting of short tangential, uniseriate lines between the wood rays. Diffuse parenchyma occurring as isolated cells or groups of cells scattered among the wood fibers. Crystalliferous strands common in some species. Parenchyma cells average 17 μ in tangential width and 81 μ in length.

Wood rays heterogeneous II B; 7 to 15 per mm., average 10. The multiseriate rays quite variable in size; range in width from 45 μ to 145 μ; 2 to 11 seriate; attain a maximum height of 2,200 μ. The ray cells of two types (tangential section): (a) small, round or oval, and (b) large and very irregular in shape. Uniseriate rays distinctive; composed of small round cells interspersed with vertically elongated cells; usually under 300 μ in height. Multi-

seriate rays with tile cells of the *Pterospermum* type. Yellowish-brown deposits common; crystals common.

Wood fibers extremely short to moderately long, average 1,093 μ in length (S.E. 10 μ, S.D. 220 μ); average middle diameter of 20 μ and wall thickness of 3 μ. Fiber long-tapering. Pits bordered; round or oval, with slitlike, extended apertures; pits 3 to 5 μ in diameter. Substitute fibers sparse to mostly lacking.

Microcos L. (1753)

Sasali Adans.; *Arsis* Lour.; *Fallopia* Lour.; *Omphacarpus* Korth.; *Inodaphnis* Miq.

Genus of about 56 species distributed in East Africa, India, Indo-China, Malaya, East Indies, and Philippines. Description based on 63 specimens representing 20 species.

Growth rings delimited by wide to narrow bands of thick-walled, radially flattened wood fibers. Rays spreading.

Pores generally oval in outline; 3 to 16 per square mm., average 6; tangential diameter range from 38 to 204 μ, average 117 μ (S.E. 1.18 μ, S.D. 24 μ); pore walls vary from 1.5 to 5, mostly about 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (45 per cent) and solitary (43 per cent), the remaining in radial multiples of 5 to 6 and tangential pairs or clusters of 3 to 9 pores; evenly distributed.

Vessel members very short to very long, average 576 μ in length (S.E. 3.32 μ, S.D. 130 μ); perforation plates simple, transverse to mostly oblique. Vessel members with short to long tails. Tyloses or gum deposits few to common.

Intervessel pit-pairs round to oval; 3 to 7 μ, mostly about 5 μ in diameter; with oval, included apertures.

Vessel-ray and vessel-parenchyma pit-pairs similar; half-bordered; round or oval, with lenticular or oval, included apertures.

Wood parenchyma terminal, paratracheal, and reticulate. The terminal consisting of interrupted uniseriate lines interspersed among the radially flattened wood fibers at the limits of the growth layers. Paratracheal parenchyma forming an incomplete uniseriate sheath or sometimes forming a complete biseriate sheath about the pores. Reticulate parenchyma abundant; forming tangential, uniseriate lines between the wood rays which are in most cases 1 to 3 fiber rows apart. Parenchyma cells average 23 μ in tangential width and 86 μ in length. The cells frequently with yellowish-brown contents or crystals.

Wood rays heterogeneous II B; 9 to 18 per mm., average 14. Multiseriate rays commonly 3 to 4, sometimes up to 6, seriate; average about 800 μ in height and reach a maximum height of

3,020 μ; width varies from 38 to 113 μ, generally under 90 μ in width. Multiseriate rays consisting of cells of two types: small, generally rounded cells forming the "shell" of the ray, and large, angular-shaped cells forming the inner portion of the ray. Tile cells of the *Durio* type present. Uniseriate rays average about 420 μ in height. Yellow-brown contents frequent; crystals sparse to common. The uniseriate rays with a tendency toward becoming storied; high rays unstoried.

Wood fibers very short to very long, average 1,498 μ in length (S.E. 10 μ, S.D. 560 μ); middle diameter average of 23 μ and wall thickness of 4.5 μ. Fibers long-tapering, sharp-pointed. Pits bordered; round or oval, with lenticular or slitlike, included or extended apertures; pits 3 to 5 μ in diameter.

Vinticena Steud. (1841)

Vincentia Boj.

Genus of about 30 species distributed in East Africa and Madagascar. Description based on one sample of *V. macromischa* Burret. (Yale No. 34015.)

Growth rings delimited by uniseriate or in part biseriate bands of terminal parenchyma accompanied by flattened wood fibers.

Pores round to oval; 20 to 37 per square mm., average 30; tangential diameter range from 38 to 113 μ, average 81 μ (S.E. 2.14 μ, S.D. 15 μ); pore walls average 5 μ in thickness. Pores solitary (43 per cent) and in radial multiples of 2 to 5 (43 per cent), the remaining in tangential pairs or clusters of 3 to 8 pores; distributed without pattern.

Vessel members extremely short to moderately short, average 263 μ in length (S.E. 2.42 μ, S.D. 24 μ); perforation plates simple, transverse to slightly oblique. Tyloses occasional; thin- to thick-walled.

Intervessel pit-pairs round; 5 to 7 μ in diameter; with small, lenticular, included apertures.

Vessel-ray pit-pairs half-bordered; generally about 5 μ in diameter; oval, with lenticular apertures extended to the margins.

Vessel-parenchyma pit-pairs half-bordered; round; 3 to 5 μ in diameter; with small, round, included apertures.

Wood parenchyma terminal and paratracheal. The terminal parenchyma consisting of uniseriate or in part biseriate bands at the limits of the growth rings. Paratracheal parenchyma sparse; accompanied by vascular tracheids and small vessels, identical in shape with vascular tracheids. Parenchyma cells average 14 μ in tangential width, 65 μ in length. Crystalliferous strands present.

Wood rays heterogeneous II B; 10 to 13 per mm., average 11. The multiseriate rays mostly 3 to 5 seriate; average 233 μ in height and 38 μ in width. Tile cells of the *Durio* and *Pterospermum* types both occur; the erect, empty cells of the *Pterospermum* type frequently crystalliferous chambered. Sheath cells present. Multiseriate rays frequently fused vertically by means of a single vertically elongated cell. Apparently it is these fusion cells which give rise to the *Pterospermum* type of tile cell as seen in this wood. Dark brown contents common. Uniseriate rays with cells of two types: small and round, and long, vertically elongated; the types alternating within the rays. In this respect the rays of *Grewia* and *Vinticena* are identical. The uniseriate rays average 219 μ in height. All elements storied.

Wood fibers extremely short to medium-sized, average 805 μ in length (S.E. 17 μ, S.D. 120 μ); average middle diameter of 14 μ and wall thickness of 3 μ. Fibers long-tapering, sharp-pointed. Pits minutely bordered; oval; up to 3 μ in diameter; with included or slightly extended, slitlike apertures.

Colona Cav. (1797)

Columbia Pers.; *Colonna* J. St. Hil.; *Diplophractum*

A genus of 25 species distributed in the East Indies, Philippine Islands, Indo-China, Malaya, and Burma. Description based on 29 specimens representing nine species.

Growth rings terminated by zones of thick-walled fibers. Wood rays spreading.

Pores round or oval; 2 to 17 per square mm., average 6; tangential diameter range from 75 to 234 μ, average 146 μ (S.E. 1.17 μ, S.D. 27 μ); tangential walls 2 to 3 μ in thickness. Pores mostly solitary (64 per cent) and in radial multiples of 2 to 3 (29 per cent), the remaining in radial multiples of 4 to 5 and in tangential pairs or clusters of 2 to 10 pores; distributed without pattern, but the pores vary somewhat in diameter from one end of the growth ring to the other.

Vessel members very short to medium-sized, average 459 μ in length (S.E. 1.75 μ, S.D. 82 μ); perforation plates simple, transverse to somewhat oblique. Tyloses and gum deposits very sparse or entirely lacking.

Intervessel pit-pairs polygonal or round to oval; diameter 5 to 8 μ; alternate; apertures lenticular, included; often coalescing.

Vessel-ray pit-pairs half-bordered; round or oval, alternate; mostly 5 to 7 μ in diameter; apertures lenticular to round and included.

Vessel-parenchyma pit-pairs half-bordered; round or oval to linear; mostly 5 to 7, up to 12, μ in diameter or length; apertures lenticular, included; alternate or irregularly disposed; frequently coalescing.

Wood parenchyma paratracheal, reticulate, and diffuse. The paratracheal forming a more or less continuous, uniseriate or biseriate sheath about the pores in the early wood; generally sparse in the late wood portion of the growth ring. Reticulate parenchyma occurring in uniseriate tangential bands between the wood rays and generally 1 to 4, up to 10, fiber rows apart. Diffuse parenchyma, when present, usually in the early wood and consisting of single isolated cells. Parenchyma cells average 23 μ in tangential width and 81 μ in length. Crystals common; cells occasionally with yellowish-brown deposits.

Wood rays heterogeneous II B; 6 to 18 per mm., average 12. Multiseriate rays 3 to 12, mostly 5 to 8, seriate; average 75 μ in width, maximum width observed was 150 μ; range in height from that of the low uniseriate rays to a maximum of 4,530 μ, but generally under 2,300 μ. Sheath cells common. Tile cells of the *Durio* type. Yellowish-brown deposits common; crystals common. Uniseriate rays generally under 750 μ in height. Low rays regularly to irregularly storied. One specimen, *C. Burretii* Kanehira, with large, radial canals, while another sample of the same species and source was without canals.

Wood fibers very short to very long, average 1,258 μ in length (S.E. 10 μ, S.D. 310 μ); middle diameter average of 27 μ, wall thickness varies from 2 to 3 μ in the early wood to 5 to 10 μ in the late wood. Pits bordered; round or oval; 3 to 5 μ in diameter; with slitlike, included or extended apertures.

Goethalsia Pittier (1914)

Monotypic genus distributed in Costa Rica, Panama, and Colombia. Description based on two specimens of *G. meiantha* (Donn. Sm.) Burret.

Growth rings delimited by 2 to 3 seriate bands of terminal parenchyma and flattened wood fibers. Rays spreading.

Pores round to oval; 3 to 12 per square mm., average 6; tangential diameter range from 75 to 174 μ, average 120 μ (S.E. 1.40 μ, S.D. 20 μ); pore walls 2 to 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (58 per cent) and solitary (40 per cent), the remaining in tangential pairs or clusters of 3 to 5 pores; evenly distributed.

Vessel members moderately short to medium-sized, average

420 μ in length (S.E. 4.97 μ, S.D. 70 μ); perforation plates simple, transverse to oblique. Gum deposits infrequent.

Intervessel pit-pairs round or oval to polygonal; 5 to 7 μ in diameter; apertures lenticular, included and frequently coalescing in pairs.

Vessel-parenchyma pit-pairs half-bordered; round or oval to irregularly rounded; 5 to 7 μ in diameter; apertures round or oval, included; alternate in arrangement.

Vessel-ray pit-pairs half-bordered; 5 to 7 μ in diameter; irregularly rounded; apertures lenticular or of the same shape as the pit outline, occasionally coalescing, included.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. Terminal parenchyma forming 1 to 3 seriate bands with the flattened wood fibers at the limits of the growth layers. Paratracheal parenchyma forming a uniseriate sheath which is invariably interrupted by the wood rays and occasionally by wood fibers. Reticulate parenchyma forming uniseriate, tangential lines between the wood rays and generally 1 to 3, up to 5, fiber rows apart. Diffuse parenchyma sparse. Parenchyma cells average 24 μ in tangential width and 87 μ in length.

Wood rays heterogeneous II B; 10 to 19 per mm., average 14. Multiseriate rays generally 5 to 8 seriate; 50 to 85 μ wide, average 65 μ; range in height from 750 to 3,850 μ, average 1,450 μ. Cells of multiseriate rays essentially similar in shape; radially elongated but with square to erect marginals. Sheath cells present. Yellowish-brown contents common; crystals not observed. Uniseriate rays average 375 μ in height; storied.

Wood fibers moderately short to moderately long, average 1,302 μ in length (S.E. 21 μ, S.D. 210 μ); average middle diameter of 25 μ and wall thickness of 1.5 to 3 μ. Fibers long-tapering, sharp-pointed. Pits bordered; round or oval; 3 to 4 μ in diameter; apertures lenticular, slitlike, included or slightly extended.

Duboscia Bocq. (1866)

Diplanthemum K. Schum.

Genus of three species distributed in the Cameroons and the Congo. Description based on one specimen of *D. macrocarpa* Bocq. (Yale No. 23238.)

Growth rings delimited by irregularly 1 to 3 seriate bands of terminal parenchyma which are more or less interrupted by flattened wood fibers. Rays spreading.

Pores round to oval; 5 to 10 per square mm., average 7; tangential diameter range from 68 to 151 μ, average 110 μ (S.E. 1.68

μ, S.D. 17 μ); pore walls average 2.5 μ in thickness. Pores mostly solitary (49 per cent) and in radial multiples of 2 to 4 (48 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 3 to 4; distributed without pattern.

Vessel members very short to medium-sized, average 396 μ in length (S.E. 7.89 μ, S.D. 80 μ); perforation plates simple, transverse to slightly inclined. Vessels without contents.

Intervessel pit-pairs round or oval; 1.5 to 3 μ in diameter; with round or oval, included apertures; frequently coalescing.

Vessel-ray and vessel-parenchyma pit-pairs similar; half-bordered; normal to unilaterally compound; the normal pit-pairs 1.5 to 3 μ in diameter, the unilaterally compound consisting of one parenchyma pit subtending 2 to 4 vessel pits.

Wood parenchyma terminal, paratracheal, and reticulate. The terminal parenchyma irregularly 1 to 3 seriate and generally interrupted by flattened wood fibers. Paratracheal parenchyma limited to the tangential faces of the pores since the wood rays generally contact the pores on both sides. Reticulate parenchyma forming short, tangential lines between the wood rays and occur 1 to 3 fiber rows apart. Parenchyma cells average 17 μ in tangential width and 82 μ in length. Cells generally without contents except near the margins of the growth rings where yellowish-brown deposits are abundant.

Wood rays heterogeneous II B; 10 to 17 per mm., average 13. Rays regularly storied with the other elements. Multiseriate rays 3 to 4 seriate and average 375 μ in height and 40 μ in width. Uniseriate rays average 262 μ in height. Cells on radial section mostly radially elongated except the marginals which are erect. Crystals most common in the marginal cells. Yellowish-brown contents common. Rays infrequently fused vertically.

Wood fibers moderately short to moderately long, average 1,418 μ in length (S.E. 33 μ, S.D. 230 μ); middle diameter average of 18 μ and wall thickness of 3.5 μ. Fibers long-tapering and sharp-pointed. Pits minutely bordered; oval; 3 to 5 μ in diameter; with slitlike, included to slightly extended apertures.

Desplatsia Bocq. (1866)

Ledermannia Mildbr. et Burret

Genus of three species distributed from Cameroons to the Belgian Congo. Description based on one sample of *D. lutea* A. Chev. (Yale No. 23252.)

Growth rings delimited by uniseriate bands of terminal parenchyma frequently interrupted by wood fibers. Rays spreading.

Pores round to oval; 4 to 8 per square mm., average 5; tangential diameter range from 53 to 174 μ, average 128 μ (S.E. 2.24 μ, S.D. 22 μ); walls 3 to 5 μ in thickness. Pores mostly in radial multiples of 2 to 4 (48 per cent) and solitary (41 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 3 to 7 pores; evenly distributed.

Vessel members very short to medium-sized, average 384 μ in length (S.E. 5.88 μ, S.D. 59 μ); perforation plates simple, transverse to slightly oblique. Deposits lacking.

Intervessel pit-pairs half-bordered; round or oval; 3 to 5 μ in diameter; with lenticular, included apertures; apertures of 2 to 3 pit-pairs frequently coalescing.

Vessel-ray and vessel-parenchyma pit-pairs similar; round or oval; diameter 5 to 7 μ; oval or lenticular, included apertures.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The terminal parenchyma forming interrupted uniseriate bands at the limits of the growth rings. Paratracheal parenchyma generally forming a complete uniseriate or in part biseriate sheath about the pores. Reticulate parenchyma forming uniseriate lines between the wood rays; the lines commonly 2 to 5 fiber rows apart. Diffuse parenchyma sparse. Cells average 20 μ in tangential width and 92 μ in length.

Rays heterogeneous II B to homogeneous I; 10 to 14 per mm., average 11. Multiseriate rays 4 to 6 seriate; average 85 μ in width and 935 μ in height. The multiseriate rays with cells of two types: (a) round or oval and thick-walled and (b) polygonal and thin-walled. The cells on radial section tabular, square, or erect. Tile cells common; of the *Durio* type. Uniseriate rays average 320 μ in height. Sheath cells present on the multiseriate rays. Crystals common in all rays. Low rays storied; the high rays in secondary seriation.

Wood fibers medium-sized to moderately long, average 1,439 μ in length (S.E. 32 μ, S.D. 230 μ); average middle diameter of 23 μ and wall thickness of 2 to 3 μ. Pits bordered; round or oval; 2 to 3 μ in diameter; with slitlike, extended apertures. Pits to ray cells 3 to 5 μ in diameter; oval; with lenticular, included apertures.

Grewiopsis De Wild. et Th. Dur. (1899)

Grewiella O. Kuntze

Genus of three (?) species distributed from Spanish Guinea to the Belgian Congo. Description based on one sample of *G. globosa* De Wild. et Th. Dur. (Yale No. 23569.)

Growth rings delimited by uniseriate or in part biseriate bands

of terminal parenchyma which are generally interrupted by wood fibers. Rays spreading.

Pores round or oval; 7 to 15 per square mm., average 11; tangential diameter range from 53 to 106 μ, average 77 μ (S.E. 1.00 μ, S.D. 10 μ); walls 2 to 3 μ thick. Pores mostly solitary (45 per cent) and in radial multiples of 2 to 4 (44 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 3 to 5 pores; well distributed.

Vessel members very short to medium-sized, average 388 μ in length (S.E. 6.16 μ, S.D. 62 μ); perforation plates simple, transverse to slightly oblique. Gum deposits present.

Intervessel pit-pairs round or oval; 3 to 5 μ in diameter; with lenticular, included apertures. Vessel-ray and vessel-parenchyma pit-pairs half-bordered; round or oval; commonly 3 μ in diameter; with oval or round, included apertures.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. Terminal parenchyma forming uniseriate or in part biseriate bands at the limits of the growth rings. Paratracheal parenchyma forming a complete uniseriate or in part biseriate sheath about the pores and appears very conspicuous on the cross section because of the large size of the cells in contrast to the wood fibers which surround the parenchyma sheaths. Reticulate parenchyma forming uniseriate lines between the wood rays; the lines commonly 2 to 5 fiber rows apart. Diffuse parenchyma sparse. Cells average 18 μ in tangential width and 101 μ in length.

Wood rays heterogeneous II B; 9 to 12 per mm., average 11. Multiseriate rays 4 to 8 seriate; range in height from 750 to 2,300 μ, average 1,320 μ; range in width from 80 to 300 μ, average 130 μ. The cells thin-walled and polygonal in outline. Sheath cells present. Tile cells of the *Durio* type. Cells on radial section mostly square or upright; tabular cells occur only in conjunction with the tile cells. Dark brown deposits common; crystals abundant. Uniseriate rays average 400 μ in height; the cells square or vertically elongated. Rays not storied.

Wood fibers medium-sized to moderately long, average 1,565 μ in length (S.E. 31 μ, S.D. 220 μ); average middle diameter of 22 μ and wall thickness of 2 to 4 μ. Pits bordered; oval; 2 to 3 μ in diameter; with oval or lenticular, included apertures.

Glyphaea Hook f. (1848)

Genus of two species distributed in tropical Africa. Description based on one sample of *G. lateriflora* Hutch. et Dalz. (Yale No. 34542.)

Growth rings delimited by 1 to 3 seriate bands of terminal parenchyma which are more or less interrupted by wood fibers. Rays spreading.

Pores round or oval but slightly angled; 6 to 12 per square mm., average 11; tangential diameter range from 53 to 106 μ, average 76 μ (S.E. 1.70 μ, S.D. 12 μ); walls 2 to 3 μ in thickness; pores well distributed. Pores mostly in radial groups of 2 to 3 (54 per cent) and solitary (33 per cent), the remaining in clusters of 3 to 6.

Vessel members very short to medium-sized, average 379 μ in length (S.E. 4.40 μ, S.D. 62 μ); perforation plates simple, transverse to slightly oblique. Deposits lacking.

Intervessel pit-pairs oval to polygonal; 2 to 3 μ in diameter; with included, lenticular apertures; alternate. Vessel-ray pit-pairs half-bordered; oval to polygonal in outline; 2 to 3 μ in diameter; with included, lenticular apertures; alternate.

Vessel-parenchyma pit-pairs unilaterally compound; quite varied in shape but generally elongated vertically. Half-bordered.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The terminal consisting of 1 to 3 seriate bands which are occasionally interrupted by wood fibers. Paratracheal parenchyma sparse; the cells made conspicuous by prominent yellowish-brown deposits. Reticulate parenchyma forming uniseriate, tangential lines between the wood rays which are generally 2 to 5 fiber rows apart. Diffuse parenchyma sparse. Parenchyma cells average 20 μ in tangential width and 106 μ in length.

Wood rays heterogeneous II A; 14 to 19 per mm., average 16. The multiseriate rays most commonly 4 to 5 seriate; average 1,130 μ in height and 83 μ in width. Cells rounded to irregular in shape on tangential section. Sheath cells common. The cells on radial section mostly square or vertically elongated; tabular cells infrequent. Uniseriate rays average 400 μ in height and 23 μ in width. Yellow-brown deposits common in all types.

Wood fibers medium-sized to moderately long, average 1,568 μ in length; middle diameter average of 18 μ and wall thickness of 3 to 5 μ. Pits bordered; oval; 3 to 5 μ in diameter; with slitlike extended apertures.

Luehea Willd. (1801)

Alegria Moc. et Sesse ex. DC.; *Brotera* Vell.

Genus of 20 species distributed throughout Central and South America (except Chile). Description based on 28 specimens representing eight species.

Growth rings limited by bands of radially flattened wood fibers or by uniseriate lines of terminal parenchyma. Rays spreading.

Pores round or oval; 8 to 17 per square mm., average 12; tangential diameter range from 45 to 196 μ, average 103 μ (S.E. 1.19 μ, S.D. 27 μ); walls average 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (58 per cent) and solitary (34 per cent), the remaining in radial multiples of 5 to 7 and in tangential pairs or clusters of 3 to 7 pores; distributed without pattern.

Vessel members extremely short to medium-sized, average 361 μ in length (S.E. 2.60 μ, S.D. 66 μ); perforation plates simple, transverse to slightly inclined. Gum deposits few to common.

Intervessel pit-pairs round or oval to polygonal; 5 to 8, mostly 7 to 8, μ in diameter; apertures oval, included, and frequently coalescing.

Vessel-ray pit-pairs half-bordered; round or oval; 3 to 5 μ in diameter, apertures round or oval, included.

Vessel-parenchyma pit-pairs half-bordered; round to irregularly rounded; 5 to 8 μ in diameter; with round or lenticular, included apertures.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The terminal parenchyma generally forming a continuous, uniseriate line at the limits of the growth rings. Paratracheal parenchyma limited to that portion of the pores not in contact with the wood rays; uniseriate or biseriate. Reticulate parenchyma forming short, uniseriate, tangential lines limited by the wood rays and in most specimens 1 to 5 fiber rows apart; the cells average 20 μ in tangential width and 86 μ in length. Diffuse parenchyma sparse.

Wood rays heterogeneous II B to homogeneous I; 9 to 16 per mm., average 12. Multiseriate rays 3 to 8, mostly 3 to 4, seriate; average 38 μ in width with a maximum of 90 μ; normal high rays reach a height of 2,100 μ; fused rays may reach a height of 2,400 μ. Uniseriate rays average 310 μ in height; storied. Multiseriate rays in secondary seriation. In some specimens multiseriate rays equal height of uniseriate rays. Tile cells of *Durio* type present. Sheath cells present. One specimen of *L. tarapotina* Macbr. (Yale No. 18807) contained numerous radial canals.

Wood fibers moderately short to very long, average 1,612 μ in length (S.E. 14 μ, S.D. 291 μ); middle diameter average of 20 μ and wall thickness of 3 μ. Fibers long-tapering, sharp-pointed. Pits bordered; oval; 3 to 7 μ in diameter; with included to slightly extended, lenticular or slitlike apertures.

Growth rings limited by bands of radially flattened wood fibers or by uniseriate lines of terminal parenchyma. Rays spreading.

Pores round or oval; 8 to 17 per square mm., average 12; tangential diameter range from 45 to 196 μ, average 103 μ (S.E. 1.19 μ, S.D. 27 μ); walls average 3 μ in thickness. Pores mostly in radial multiples of 2 to 4 (58 per cent) and solitary (34 per cent), the remaining in radial multiples of 5 to 7 and in tangential pairs or clusters of 3 to 7 pores; distributed without pattern.

Vessel members extremely short to medium-sized, average 361 μ in length (S.E. 2.60 μ, S.D. 66 μ); perforation plates simple, transverse to slightly inclined. Gum deposits few to common.

Intervessel pit-pairs round or oval to polygonal; 5 to 8, mostly 7 to 8, μ in diameter; apertures oval, included, and frequently coalescing.

Vessel-ray pit-pairs half-bordered; round or oval; 3 to 5 μ in diameter, apertures round or oval, included.

Vessel-parenchyma pit-pairs half-bordered; round to irregularly rounded; 5 to 8 μ in diameter; with round or lenticular, included apertures.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The terminal parenchyma generally forming a continuous, uniseriate line at the limits of the growth rings. Paratracheal parenchyma limited to that portion of the pores not in contact with the wood rays; uniseriate or biseriate. Reticulate parenchyma forming short, uniseriate, tangential lines limited by the wood rays and in most specimens 1 to 5 fiber rows apart; the cells average 20 μ in tangential width and 86 μ in length. Diffuse parenchyma sparse.

Wood rays heterogeneous II B to homogeneous I; 9 to 16 per mm., average 12. Multiseriate rays 3 to 8, mostly 3 to 4, seriate; average 38 μ in width with a maximum of 90 μ; normal high rays reach a height of 2,100 μ; fused rays may reach a height of 2,400 μ. Uniseriate rays average 310 μ in height; storied. Multiseriate rays in secondary seriation. In some specimens multiseriate rays equal height of uniseriate rays. Tile cells of *Durio* type present. Sheath cells present. One specimen of *L. tarapotina* Macbr. (Yale No. 18807) contained numerous radial canals.

Wood fibers moderately short to very long, average 1,612 μ in length (S.E. 14 μ, S.D. 291 μ); middle diameter average of 20 μ and wall thickness of 3 μ. Fibers long-tapering, sharp-pointed. Pits bordered; oval; 3 to 7 μ in diameter; with included to slightly extended, lenticular or slitlike apertures.

Luehopsis Burret (1926)

Genus of eight species distributed in Brazil and Dutch Guiana. Description based on four specimens representing three species.

Growth rings delimited either by bands of radially flattened wood fibers or by uniseriate bands of terminal parenchyma. Rays spreading.

Pores oval to round and very slightly angled; 0 to 5 per square mm., average 3; tangential diameter range from 60 to 264 μ, average 169 μ (S.E. 2.11 μ, S.D. 37 μ); walls average 4 μ in thickness. Pores mostly solitary (54 per cent) and in radial multiples of 2 to 4 (39 per cent), the remaining in tangential pairs or clusters of 3 to 5 pores; evenly distributed.

Vessel members very short to medium-sized, average 440 μ in length (S.E. 2.50 μ, S.D. 44 μ); perforation plates simple, transverse to slightly inclined. Gum deposits occasional.

Intervessel pit-pairs round or oval to polygonal; 5 to 7 μ in diameter; apertures round or oval to lenticular, included, frequently coalescing.

Vessel-ray and vessel-parenchyma pit-pairs identical; normal or unilaterally compound; the normal 3 to 5 μ in diameter, the unilaterally compound consisting of one parenchyma pit subtending 2 to 4 vessel pits; apertures of normal pits round; apertures of compound pits flattened-oval in shape, extending almost to the pit margins.

Wood parenchyma terminal, paratracheal, reticulate, paratracheal-banded, and diffuse. Terminal parenchyma forming more or less continuous 1 to 3 seriate bands which are generally interspersed with flattened wood fibers. Paratracheal parenchyma mostly limited to the portion of the pores not in contact with the wood rays or sometimes forming a complete uniseriate sheath about the pores. Reticulate parenchyma in uniseriate or biseriate lines between the wood rays. Paratracheal-banded in short to long, tangential lines 2 to 4 seriate; the lines continuous across the wood rays. Diffuse parenchyma found as isolated cells or groups at the ends of the bands or between them. Parenchyma cells average 25 μ in width and 102 μ in length. Frequently with yellowish-brown contents or starch grains which are round and up to 17 μ in diameter.

Wood rays heterogeneous II B to homogeneous I; average 10 per mm. Multiseriate rays mostly 3 to 5, up to 7, seriate; average 1,300 μ in height and 60 μ in width. Uniseriate rays average 332 μ in height; regularly storied; the high rays in secondary seriation.

Tile cells of the *Durio* type present; sheath cells present. Cells with yellowish-brown contents.

Wood fibers medium-sized to very long, average 1,707 μ in length (S.E. 19 μ, S.D. 230 μ); middle diameter average of 23 μ and wall thickness of 5 μ. Fibers long-tapering, sharp-pointed. Pits bordered; oval; 5 to 8 μ in diameter; with slightly extended to included apertures.

Mollia Mart. (1824)

Schlechtendalia Spreng.

Genus of nine species in northern South America. Description based on two specimens of two species.

Growth rings defined by narrow bands of radially flattened wood fibers. Rays spreading at limits of growth rings.

Pores round or oval and very slightly angled; 3 to 9 per square mm., average 6; tangential diameter range from 53 to 166 μ (S.E. 1.40 μ, S.D. 17 μ); pore walls average 4.5 μ in thickness. Pores mostly in radial multiples of 2 to 4 (69 per cent) and solitary (17 per cent), the remaining in radial multiples of 5 or 6 and tangential pairs or clusters of 3 pores; well distributed.

Vessel members very short to medium-sized, average 438 μ in length (S.E. 5.42 μ, S.D. 54 μ); perforation plates simple, transverse to slightly oblique. Gum deposits occasional.

Intervessel pit-pairs round or oval; 2 to 3 μ in diameter; with oval, included apertures which frequently coalesce; alternate.

Vessel-ray and vessel-parenchyma pit-pairs half-bordered; like the intervessel in size and shape.

Wood parenchyma paratracheal, paratracheal-banded, and diffuse. The paratracheal parenchyma forming a complete uniseriate sheath about the pores. Paratracheal-banded parenchyma generally irregular, 1 to 6 seriate, and usually forming short lines between the pores or extensions from them. Reticulate parenchyma occasionally like the banded and consisting of uniseriate or biseriate lines between the wood rays or sometimes continuous across several rays. Diffuse parenchyma sparse. Parenchyma cells average 22 μ in tangential width and 99 μ in length. Crystals common; crystalliferous strands frequently interspersed among the multiseriate bands of parenchyma.

Wood rays heterogeneous II B to homogeneous I; 9 to 14 per mm., average 11. Multiseriate rays commonly 3 to 4 seriate; the normal multiseriate high rays average 700 μ in height and 38 to 68 μ in width; vertically fused rays may reach a height of 1,960 μ. Tile cells abundant; of the *Durio* type. Sheath cells sparse. Body

cells of the multiseriate rays mostly tabular with erect marginals. Uniseriate rays average 310 μ in height; regularly storied. High rays in secondary seriation. Yellowish-brown deposits and crystals common.

Wood fibers moderately short to moderately long, average 1,263 μ in length (S.E. 19 μ, S.D. 140 μ); middle diameter average of 19 μ and wall thickness of 3 μ. Pits bordered; oval; 2 to 5 μ in diameter; with slitlike, extended apertures.

Trichospermum Bl. (1825)

Declidocarpus A. Gray; *Bixagrewia* Kurz; *Halconia* Merr.; *Grewia* auct.

Genus of nine species distributed in the Philippines, East Indies, Malaya, and the South Pacific Islands to Fiji and Samoa. Description based on 17 specimens representing seven species.

Growth rings, when present, defined by bands of terminal parenchyma; the cells radially flattened and in bands which are 6 to 10 seriate.

Pores round or slightly oval; 2 to 9 per square mm., average 5; tangential diameter range from 45 to 196 μ, average 131 μ (S.E. 2.42 μ, S.D. 24 μ); pore walls average 2.5 μ in thickness. Pores mostly solitary (78 per cent) and in radial multiples of 2 to 4 (17 per cent), the remaining in tangential pairs or clusters of 3 to 4 pores; evenly distributed.

Vessel members very short to moderately long, average 544 μ in length (S.E. 10.58 μ, S.D. 106 μ); perforation plates simple, slightly oblique to very oblique. Tyloses occasional.

Intervessel pit-pairs round or oval to polygonal; 10 to 12 μ in diameter; with oval, included apertures.

Vessel-ray and vessel-parenchyma pit-pairs half-bordered; irregularly rounded to lenticular; 8 to 12 μ in diameter; apertures of the same shape as the pit outline and extended to the pit margins.

Wood parenchyma terminal, paratracheal, and diffuse. The terminal as described under growth rings. Paratracheal parenchyma generally forming a complete biseriate sheath about the pores. Diffuse parenchyma consisting of isolated cells or pairs in the vicinity of the pores; infrequently forming short lines of 3 to 4 cells between the rays. Cells average 26 μ in tangential width and 132 μ in length. Without contents.

Wood rays heterogeneous II B; 6 to 13 per mm., average 10. Multiseriate rays commonly 3 to 6 seriate; in some specimens 5 to 9 seriate. High rays average 1,668 μ in height and 63 to 151 μ in width; maximum height of 2,600 μ and width of 204 μ. Uniseriate

rays average 468 μ in height. Rays cells with brownish contents; crystals abundant to sparse. Sheath cells present; in *T. discolor* Elmer, sheath cells form the "shell" of the large rays.

Wood fibers moderately short to moderately long, average 1,351 μ in length (S.E. 14 μ, S.D. 220 μ); middle diameter average 28 μ and wall thickness of 2 to 5 μ. Pits bordered; oval to round; 2 to 5 μ in diameter; with included to slightly extended, lenticular or slitlike apertures.

Belotia A. Rich. (1845)

Adenodiscus Turcz.

Monotypic genus distributed in Cuba, British Honduras, Panama, Mexico, and northern South America. Description based on 13 specimens of *B. grewiifolia* A. Rich.

Growth rings generally lacking or, when present, only weakly differentiated by terminal parenchyma. Wood rays not spreading.

Pores round to oval; 2 to 15, mostly 4 to 8, per square mm.; tangential diameter range from 75 to 311 μ, average 138 μ (S.E. 1.12 μ, S.D. 19 μ); pore walls 2 to 3 μ in thickness. Pores mostly solitary (60 per cent) and in radial multiples of 2 to 4 (34 per cent), the remaining in radial multiples of 5 to 7 and in tangential pairs or clusters of 3 to 7 pores; evenly distributed.

Vessel members moderately short to moderately long, average 556 μ in length (S.E. 2.54 μ, S.D. 88 μ); perforation plates simple, transverse to somewhat oblique. Tyloses sparse or lacking; rarely thick-walled. Gum deposits observed only in conjuction with pith flecks.

Intervessel pit-pairs polygonal or round to oval; 7 to 10 μ in diameter; apertures oval or lenticular to slitlike, included, infrequently coalescing.

Vessel-ray and vessel-parenchyma pit-pairs similar; half-bordered; 5 to 13 μ in diameter; apertures of the same shape as the pit outline, included; alternate.

Wood parenchyma terminal, paratracheal, and diffuse. The terminal, when present, forming a somewhat interrupted band up to 5 seriate. Paratracheal parenchyma forming a more or less continuous sheath about the pores when not interrupted by the wood rays. Diffuse parenchyma abundant, consisting of single cells or pairs scattered throughout the growth layers. Cells average 25 μ in tangential width and 124 μ in length. Without contents.

Wood rays heterogeneous II B; 7 to 12 per mm., average 9. Multiseriate rays commonly 3 to 5, sometimes 6, seriate; average 1,350 μ in height and 65 μ in width. Vertical fusions common.

Tile cells of the *Durio* type present. Sheath cells present. Uniseriate rays mostly between 400 and 600 μ in height. Yellowish-brown deposits common in all rays.

Wood fibers very short to moderately long, average 1,213 μ in length (S.E. 12 μ, S.D. 280 μ); middle diameter average of 35 μ; walls 2 to 3 μ thick. Fibers tapering gradually or abruptly at ends. Pits bordered; round or oval; 2 to 3 μ in diameter; with slitlike, extended apertures.

Althoffia K. Schum. (1888)

Genus of five species distributed in the Philippines, East Indies, and Queensland. Description based on one sample of *A. lanigera* (Blanco) Burret. (Bureau of Forestry, Manila No. 21046.)

Growth rings lacking.

Pores oval to angular; 0 to 4 per square mm.; tangential diameter range from 75 to 211 μ, average 146 μ (S.E. 2.84 μ, S.D. 28 μ); pore walls 1 to 1.5 μ thick. Pores mostly solitary (89 per cent) and in radial multiples of 2 to 3 (11 per cent); well distributed.

Vessel members medium-sized to moderately long, average 692 μ in length (S.E. 12.56 μ, S.D. 126 μ); perforation plates simple, never transverse; tails short to long; tyloses sparse.

Intervessel pit-pairs round or oval to polygonal; 7 to 12 μ in diameter, commonly 10 μ; apertures round, included; alternate.

Vessel-ray pit-pairs bordered to half-bordered; round or oval; 7 to 10 μ in diameter; with large apertures of the same shape as the pit outline; included.

Wood parenchyma sparse; paratracheal and diffuse. The paratracheal consisting generally of several cells in contact with the pore. Paratracheal parenchyma consisting of isolated cells or short lines in the immediate vicinity of the pores. Cells average 37 μ in tangential width and 98 μ in length. Crystals occasionally present.

Wood rays heterogeneous II A; 4 to 8 per mm., average 6. Multiseriate rays 3 to 6, mostly 5 to 6, seriate; average 1,200 μ in height and 112 μ in width. Sheath cells present. Uniseriate rays average 535 μ in height. Ray cells commonly with yellowish deposits. Crystals sparse. Rays unstoried.

Wood fibers moderately short to moderately long, average 1,348 μ in length (S.E. 20 μ, S.D. 180 μ); average middle diameter of 46 μ; walls 1 to 1.5 μ thick. Fibers short-tapering. Pits bordered; oval; 2 to 4 μ in diameter; with slitlike, extended apertures.

Erinocarpus Nimmo ex J. Graham (1839)

Monotypic genus distributed in India. Description based on two specimens of *E. Nimmoanus* J. Graham.

Growth rings delimited by terminal parenchyma which is 1 to 4 seriate and merges frequently with the paratracheal-banded parenchyma. Rays spreading at growth ring limits.

Pore round or oval to slightly angular; 6 to 18 per square mm., average 10; tangential diameter range from 53 to 211 μ, average 128 μ (S.E. 2.43 μ, S.D. 34 μ); walls generally 3 μ in thickness. Pores mostly solitary (82 per cent) and in radial multiples of 2 to 4 (13 per cent), the remaining in tangential pairs; evenly distributed.

Vessel members moderately short to medium-sized, average 395 μ in length (S.E. 3.31 μ, S.D. 47 μ); perforation plates simple, transverse to slightly inclined. Tyloses present.

Vascular tracheids occur sparingly among the paratracheal-banded parenchyma strands. Although being mostly imperforate, some tracheids have perforations at one or rarely at both ends. The tracheids are of the same length as the parenchyma strands and are indistinguishable from them on the cross section. The tracheids possess pits like those of the vessel members but are somewhat smaller in size; occasionally scalariform.

Intervessel pit-pairs round or oval to polygonal; 7 to 10 μ in diameter; apertures narrowly lenticular, included; the apertures of 2 to 4 adjacent pits frequently coalescing.

Vessel-ray pit-pairs half-bordered; oval or round to flattened-lenticular; 4 to 12 μ in diameter or length; with included, lenticular, or slitlike, extended apertures.

Vessel-parenchyma pit-pairs half-bordered; oval; 5 to 10 μ in diameter; with lenticular, included apertures or with very slightly extended apertures.

Wood parenchyma terminal, paratracheal, paratracheal-banded, and diffuse. Paratracheal parenchyma frequently forming a 3 or more seriate sheath about the pores. Paratracheal-banded parenchyma irregularly banded. Diffuse parenchyma occurring as single isolated cells or short tangential lines either at the ends of the paratracheal bands or between them. Cells average 27 μ in tangential diameter and 127 μ in length; walls 1.5 μ in thickness. Crystalliferous strands common.

Wood rays heterogeneous II A; 3 to 7 per mm., average 5. Multiseriate rays commonly 4 to 5, sometimes 6, seriate; generally under 2,200 μ in height and reach a maximum height of 4,000 μ; average 90 μ in width, maximum observed, 115 μ. Uniseriate

rays average 500 μ in height. Ray cells generally without contents. Rays unstoried.

Wood fibers medium-sized to very long, average 1,799 μ in length (S.E. 19 μ, S.D. 200 μ); average middle diameter of 23 μ; wall thickness of 7 μ. Pits bordered; oval; 3 to 5 μ in diameter; with slitlike extended apertures.

Triumfetta L. (1753)

Ceratosepalum Oliv.

Genus of about 50 species distributed throughout the tropics of both hemispheres. Description based on 12 specimens representing five species.

Growth rings defined by bands of terminal parenchyma which are irregularly 1 to 4 seriate or by isolated parenchyma cells and flattened wood fibers. Wood rays spreading at limits of growth rings.

Pores angular in cross-sectional outline; 12 to 36 per square mm., average 25; tangential diameter range from 38 to 91 μ, average 66 μ (S.E. 1.71 μ, S.D. 12 μ); walls 1.5 to 3 μ in thickness. Pores mostly solitary (60 per cent) and in radial multiples of 2 to 4 (34 per cent) the remaining in radial multiples of 5 to 8 and in tangential pairs or clusters of 3 to 5 pores; evenly distributed.

Vessel members extremely short to medium-sized, average 426 μ in length (S.E. 3.68 μ, S.D. 82 μ); perforation plates simple, obliquely inclined; without deposits.

Intervessel pit-pairs rounded or polygonal; 8 to 10 μ in diameter; with oval, included apertures which are at times almost slitlike.

Vessel-ray pit-pairs half-bordered; ovate to irregular in outline; 7 to 16 μ wide, mostly 8 to 10 μ wide; alternate; apertures large, and of the same shape as the pit outline.

Vessel-parenchyma pit-pairs half-bordered; oval; generally about 8 μ in diameter; apertures large, included.

Wood parenchyma terminal and paratracheal. The paratracheal generally sparse.

The wood of this genus possesses a specialized type of parenchyma characterized by very thin walls, lack of contents, and its relative abundance. It is generally disposed in small islands, short to long tangential bands or arcs, or wide tangential bands of variable width. The rays in passing through these areas of thin-walled parenchyma become very much reduced in width. This type of parenchyma also occurs in the woods of *Heliocarpus, Entelea,* and *Apeiba.*

Wood rays heterogeneous I to heterogeneous II A; 9 to 17 per mm., average 13. Multiseriate rays 3 to 6 seriate; average 1,200 μ in height and 70 μ in width. The ray cells mostly upright, square or radially elongated; the upright cells mostly marginal. Sheath cells present. Starch grains, crystals, and a small amount of yellowish deposits present. Ray cells containing crystals are usually chambered. The uniseriate rays exhibit a definite tendency toward becoming storied.

Wood fibers very short to medium-sized, average 1,137 μ in length (S.E. 19 μ, S.D. 190 μ); middle diameter average of 22 μ; wall thickness average of 4 μ. Pits bordered; oval; up to 3 μ in diameter; with included or very slightly extended slitlike apertures. Inner walls of fibers mucilaginous or with a definite tendency toward that condition.

Heliocarpus L. (1753)

Genus of about 14 species distributed throughout the tropics of the Western Hemisphere. Description based on 23 specimens representing six species.

Growth rings lacking or, when present, defined by bands of terminal parenchyma which are irregularly 2 to 14 seriate; the cells radially flattened.

Pores round or oval to very slightly angled; 1 to 7 per square mm., average 3 or 4; tangential diameter range from 60 to 242 μ, average 143 μ (S.E. 6.38 μ, S.D. 79 μ); pore walls 1 to 2.5 μ in thickness. Pores mostly solitary (51 per cent) and in radial multiples of 2 to 4 (41 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 3 to 7 pores; evenly distributed.

Vessel members moderately short to medium-sized, average 446 μ in length (S.E. 3.24 μ, S.D. 78 μ); perforation plates simple, transverse or slightly oblique to very oblique. Tyloses occasional.

Intervessel pit-pairs polygonal; 8 to 17, mostly 8 to 12, μ in diameter; with oval or lenticular, included apertures; alternate.

Vessel-ray pit-pairs half-bordered; oval or lenticular; 8 to 18 μ in diameter or length; with large apertures of the same shape as the pit outline.

Vessel-parenchyma pit-pairs half-bordered; round or oval; 5 to 13 μ in diameter; with large, included apertures of the same shape as the pit.

Wood parenchyma terminal, reticulate, and paratracheal. The paratracheal generally forming a uniseriate or in part biseriate sheath about the pores. Reticulate parenchyma consisting of uni-

seriate or in part biseriate lines between the wood rays and spaced 1 to 3 fiber rows apart. Parenchyma cells average 26 μ in tangential width and 122 μ in length. Contents generally sparse or lacking.

Specialized thin-walled parenchyma abundant; occurring in small islands, irregular concentric arcs, or in concentric tangential bands of varying width; frequently up to several millimeters in width. The cells polygonal in cross-sectional outline and axially elongated as seen from the tangential and radial sections. Rays passing through these areas of thin-walled parenchyma become constricted. The wide bands of parenchyma frequently engulf solitary pores but the majority of pores occur in the fibrous portion of the cross section.

Wood rays heterogeneous II B; 6 to 11 per mm., average 9. Multiseriate rays commonly 4 to 5 seriate; average 1,300 μ in height and 58 μ in width. Cells square, erect or radially elongated as seen on radial section; sometimes almost tilelike in appearance. Uniseriate rays irregularly storied and very variable in height; ranging from 250 to 1,400 μ in height; normal uniseriate rays average about 400 μ in height. Chambered crystalliferous ray cells occasional. Ray cells with or without yellowish-brown contents.

Wood fibers medium-sized to very long, average 1,479 μ in length (S.E. 13 μ, S.D. 220 μ); average middle diameter of 28 μ; walls 1.5 to 3 μ in thickness. Fibers sharp-pointed, short-tapering; frequently bifurcated. Pits bordered; oval or round; 3 to 7 μ in diameter; with extended, slitlike apertures.

Honckenya Willd. (1793)

Clappertonia Meissn.
Cephalonema K. Schum. ex Sprague

Genus of three species distributed in Africa from Liberia to Nyassa. Description based on one small stem of *H. ficifolia* Willd. (Harvard No. 19404.)

Growth rings delimited by radially flattened, thick-walled wood fibers.

Pores angular on cross section; 8 to 16 per square mm., average 12; tangential diameter range from 45 to 91 μ, average 66 μ (S.E. 1.55 μ, S.D. 11 μ); pore walls 1 to 1.5 μ in thickness. Pores mostly solitary (59 per cent) and in radial multiples of 2 to 5 (26 per cent), the remaining in tangential pairs or clusters of 3 to 5 pores.

Vessel members moderately short to medium-sized, average

404 μ in length (S.E. 11.38 μ, S.D. 114 μ); perforation plates simple, obliquely inclined. Without contents.

Intervessel pit-pairs round or oval; 8 to 10 μ in diameter; with lenticular, included apertures.

Vessel-ray and vessel-parenchyma pit-pairs half-bordered; round or oval; 8 to 10 μ in diameter; with lenticular apertures the ends of which extend to the pit margins.

Wood parenchyma sparse paratracheal.

Wood rays heterogeneous I; 9 to 13 per mm., average 11. Multiseriate rays mostly 2 to 3 seriate and average 53 to 65 μ in width. Rays extremely variable in height, reaching a height of 3,020 μ, but are generally under 2,500 μ. Cells square to rectangular or erect. Uniseriate rays of the same height as the multiseriate. Yellowish-brown contents common.

Wood fibers extremely short to very short; average 496 μ in length (S.E. 10 μ, S.D. 65 μ); average middle diameter of 28 μ and wall thickness of 1 to 1.5 μ. Fibers abruptly tapering; the extensions very short. Pits bordered; 3 to 5 μ in diameter; oval; with slitlike, extended apertures.

Entelea R. Br. (1824)

Apeiba A. Rich.

Monotypic genus of New Zealand and Australia. Description based on one sample of *E. arborescens* R. Br. (Harvard No. 16529.)

Growth rings not observed.

Pores round or oval to angular; 2 to 8 per square mm., average 5; tangential diameter range from 30 to 143 μ, average 89 μ (S.E. 1.89 μ, S.D. 19 μ); walls average 1.5 μ in thickness. Pores mostly solitary (60 per cent) and in radial multiples of 2 to 4 (35 per cent), the remaining in tangential pairs or clusters of 3 to 5 pores; evenly distributed.

Vessel members extremely short to medium-sized, average 332 μ in length (S.E. 6.04 μ, S.D. 60 μ); perforation plates simple; obliquely inclined. Tyloses sparse.

Intervessel pit-pairs polygonal; 8 to 17, mostly 8 to 12, μ in diameter; with included, oval apertures. Some vessel members exhibit a tendency toward opposite arrangement of the intervessel pit-pairs especially near the ends of the members.

Vessel-ray pit-pairs half-bordered; oval; mostly 8 to 12 μ in diameter; apertures included, of the same shape as the pit outline.

Vessel-parenchyma pit-pairs half-bordered; oval; 8 to 17 μ in diameter; oval, included apertures.

Wood parenchyma paratracheal and diffuse; both types sparse.

Cells average 26 μ in tangential width and 129 μ in length; without contents.

A specialized type of thin-walled parenchyma also occurs in this genus which resembles markedly that found in the genus *Apeiba,* but differing from *Apeiba* in that the parenchyma is not so abundant and the cells are not as long in radial length.

Wood rays heterogeneous II A; 7 to 10 per mm. Multiseriate rays commonly 5 to 8, sometimes up to 12 seriate; average 105 μ in width but reach a width of 242 μ; average 1,240 μ in height and attain a maximum of 4,000 μ. Sheath cells present. Cells on radial section mostly square or radially elongated to erect; small amount of yellowish-brown deposits present; crystals lacking.

Wood fibers very short to medium-sized, average 923 μ in length (S.E. 46 μ, S.D. 320 μ); average middle diameter of 40 μ and with a wall thickness of 1.5 μ. Fibers short-tapering; body well defined; frequently very irregular in shape. Pits bordered; oval; 3 to 7 μ in diameter; with lenticular or slitlike, extended apertures.

Apeiba Aubl. (1775)

Genus of five species distributed in tropical America. Description based on 19 specimens representing five species.

Growth rings delimited by uniseriate or in part biseriate lines of terminal parenchyma. Wood rays spreading.

Pores round to very oval; 1 to 10 per square mm.; tangential diameter range from 75 to 302 μ, average 151 μ (S.E. 0.92 μ, S.D. 30 μ); walls generally 2 to 4 μ in thickness. Pores mostly solitary (60 per cent) and in radial multiples of 2 to 4 (35 per cent), the remaining in radial multiples of 5 to 6 and in tangential pairs or clusters of 3 to 9 pores; evenly distributed.

Vessel members very short to moderately long, average 491 μ in length (S.E. 1.77 μ, S.D. 78 μ); perforation plates simple; slightly oblique to oblique; tyloses sparse or lacking; gum deposits occasional.

Intervessel pit-pairs round or oval to polygonal; 5 to 8 μ in diameter; apertures oval or lenticular to slitlike, included; infrequently coalescing or extended.

Vessel-ray pit-pairs round or oval to unilaterally compound; half-bordered; the normal pits 5 to 8 μ in diameter, the unilaterally compound much larger.

Vessel-parenchyma pit-pairs half-bordered; irregularly rounded to oval; 5 to 8 μ in diameter; with lenticular or oval, included apertures.

Wood parenchyma terminal, paratracheal, reticulate, and diffuse. The paratracheal forming a more or less continuous, uniseriate or in part biseriate sheath about the pores. The reticulate forming uniseriate, tangential lines between the wood rays and the lines alternate with 1 to 6 fiber rows. Diffuse parenchyma present as isolated cells which occur most commonly in the early wood of wide growth rings. In young stems the diffuse parenchyma is the dominant type. Cells average 28 μ in tangential width and 98 μ in length. Crystals common to abundant.

The woods of this genus possess the thin-walled parenchyma described previously for *Entelea, Heliocarpus,* and *Triumfetta.* This tissue occurs in islands, short arcs, or in concentric bands of varying width up to 5 mm. Wood rays which pass through these areas become very much contricted. The cells are radially elongated and sometimes reach a length of 450 μ.

Wood rays heterogeneous II B; 6 to 14 per mm., average 10. Multiseriate rays 3 to 10 seriate; average 1,300 μ in height and 90 μ in width. Cells of the multiseriate rays are small and round, or oval and large and polygonal in outline. Sheath cells present. Crystals usually abundant. Uniseriate rays vary considerably in height but are generally about 450 μ in height and in most specimens are irregularly storied.

Wood fibers moderately short to very long, average 1,525 μ in length (S.E. 13 μ, S.D. 390 μ); middle diameter average of 30 μ and wall thickness of 2 to 3 μ. Fibers long-tapering; infrequently bifurcated. Pits bordered; round or oval; with lenticular or slit-like extended apertures. Pits 2 to 3 μ in diameter.

DESCRIPTION OF THE WOODS OF THE ELAEOCARPACEAE

Sloanea L. (1753)

Ablania Aubl.; *Trichocarpus* Schrb.; *Dasynema* Schott.; *Adenobasium* Prsl.; *Foveolaria* Meissn.; *Dasycarpus* Oerst.; *Blondea* L.C. Rich.; *Leiostemon* Moc. et Sesse; *Echinocarpus* Bl.; *Phoenicospermum* Miq.

Genus of about 44 species distributed throughout the tropics of both hemispheres. Description based on 10 samples of four species.

Growth rings bounded by narrow flattened wood-fibre bands.

Pores angular; 10 to 27 per square mm., average 18; tangential diameter range from 38 to 143 μ, average 82 μ (S.E. 3.00 μ, S.D. 42 μ); walls average 3 μ in thickness. Pores mostly solitary (60 per cent) and in radial multiples of 2 to 4 (29 per cent), the remaining in tangential pairs or clusters of 3 to 5 pores; evenly distributed.

Vessel members moderately short to very long, average 837 μ in length (S.E. 6.03 μ, S.D. 191 μ); perforation plates simple or occasionally vestigial scalariform; obliquely inclined. Tyloses present. Vessel members with short to long tails.

Intervessel pit-pairs round or oval to square and polygonal; 8 to 15, mostly 8 to 10, μ in diameter; with small, oval, included apertures; opposite in arrangement.

Vessel-ray pit-pairs half-bordered to fully-bordered; transitional to scalariform and up to 40 μ in length; with large apertures.

Vessel-parenchyma pit-pairs like the vessel-ray pit-pairs.

Wood parenchyma sparse; paratracheal and diffuse. The cells average 21 μ in tangential width and 118 μ in length. Without contents.

Wood rays heterogeneous II A; 7 to 17 per mm., average 10. Multiseriate rays 1 to 6, mostly 3 to 5, seriate; mostly 35 to 50 μ in width and 500 to 750 μ in height. Uniseriate rays quite high, but usually lower than the multiseriate. Yellowish-brown contents and crystals common.

Wood fibers moderately short to very long, average 1,454 μ in length (S.E. 12 μ, S.D. 270 μ); average middle diameter of 25 μ and wall thickness of 2.5 μ. Fibers short to long-tapering; in part septate. Fiber pits bordered; oval; with slitlike, extended apertures.

Elaeocarpus L. (1753)

Ganitrus Gartn.; *Monocera* Jack.; *Dicera* Forst.; *Adenodus* Lour.; *Craspedum* Lour.; *Aceratium* DC.; *Beythia* Lindl.; *Acronodia* Bl.; *Acrozus* Spr.; *Lochneria* Scop.; *Perinkara* Adans.

Genus of about 60 species distributed in India, China, Malaya, Siam, Japan, Australia, New Zealand, New Caledonia, and Hawaii. Description based on 41 specimens representing 31 species.

Growth rings delimited by uniseriate or in part biseriate bands of terminal parenchyma or in some species only by bands of flattened wood fibers. Rays spreading.

Pores round to oval; average 4 per square mm.; tangential diameter range from 113 to 219 μ, average 168 μ (S.E. 2.99 μ, S.D. 21 μ); pore walls 3 to 4 μ in thickness. Pores mostly solitary (65 per cent) and in radial multiples of 2 to 5 (28 per cent), the remaining in tangential pairs or clusters of 3 to 6 pores; evenly distributed.

Vessel members medium-sized to very long, average 808 μ in length (S.E. 5.39 μ, S.D. 172 μ); perforation plates simple; oblique. Contents generally sparse. Tertiary spirals present in some species.

Intervessel pit-pairs round or oval; 10 to 20, mostly 15 to 17, μ in diameter; with included, lenticular apertures.

Vessel-ray pit-pairs half-bordered; irregularly rounded and up to 24 μ in diameter, generally about 17 μ in diameter; apertures large, of the same shape as the pit outline.

Wood parenchyma terminal and paratracheal. The terminal, 1 to 3 seriate, more or less continuous and frequently interspersed with flattened wood fibers. Paratracheal parenchyma very sparse. Cells average 26 μ in tangential width and 156 μ in length.

Wood rays heterogeneous I; 14 to 21 per mm., average 17. The multiseriate rays usually 3 to 5 seriate and average 38 μ in width; average 910 μ in height. Uniseriate rays average 605 μ in height. Cells mostly tabular except the marginals which are square to erect. Crystals abundant; brown deposits common.

Wood fibers very short to moderately long, average 1,424 μ in length (S.E. 8 μ, S.D. 226 μ); middle diameter average of 27 μ and wall thickness of 3 μ. Pits bordered; up to 5 μ in diameter; oval; with slitlike extended apertures. Septate and substitute fibers present in some species.

Vallea Mutis. (1781)

Genus of three species distributed in Peru. Description based on two samples representing two species.

Growth rings defined by narrow bands of radially flattened wood fibers.

Pores angular; 31 to 63 per square mm., average 50; tangential diameter range from 25 to 91 μ, average 48 μ (S.E. 1.64 μ, S.D. 11 μ); walls average 1.5 μ in thickness; evenly distributed. Pores mostly in radial multiples or chains which may extend across an entire growth ring.

Vessel members medium-sized to moderately long, average 638 μ in length (S.E. 7.49 μ, S.D. 106 μ); perforation plates mostly simple, infrequently vestigial scalariform and obliquely inclined. Tyloses sparse.

Intervessel pit-pairs round or oval to scalariform; 8 to 15 μ in diameter or length; with lenticular, included apertures; alternate to transitional.

Vessel-ray pit-pairs half-bordered; 8 to 28 μ in diameter or length; opposite to scalariform; apertures of the same shape as the pit outline.

Wood parenchyma lacking.

Wood rays heterogeneous II B; 10 to 18 per mm., average 15. Rays 1 to 3 seriate; average 1,132 μ in height and 23 to 37 μ in

width. Uniseriate rays variable in height from 300 to 1,100 μ. Sheath cells present.

Wood fibers extremely short to medium-sized, average 791 μ in length (S.E. 33 μ, S.D. 120 μ); average middle diameter of 20 μ and wall thickness of 3.5 μ. Fibers short-tapering. Square to hexagonal on cross section. Pits bordered; 2 to 5 μ in diameter; round or oval; apertures lenticular, included or slightly extended.

Aristotelia L'Herit. (1784)

Friesea DC.

Genus of seven species distributed in Australia, New Zealand, and Chile. Description based on three specimens (two species).

Growth rings defined by narrow bands of radially flattened wood fibers. Rays spreading.

Pores angular; 20 to 84 per square mm., average 59; tangential diameter range from 23 to 98 μ, average 55 μ (S.E. 1.05 μ, S.D. 13 μ); pore walls average 2 μ in thickness. Pores mostly solitary (50 per cent) in tangential pairs or clusters of 3 to 5 pores (28 per cent) and in radial multiples of 2 to 4 (18 per cent), the remaining in radial multiples of 5 to 7 and clusters of 6 to 8 pores; largest pores in early wood portion of growth ring, tending to assume a somewhat ring-porous or semi-ring porous condition.

Vessel members moderately short to moderately long, average 500 μ in length (S.E. 5.75 μ, S.D. 100 μ); perforation plates simple to vestigial scalariform; tails short to long. Tyloses present.

Intervessel pit-pairs round or oval to transitional and scalariform; apertures oval, included; mostly about 8 μ in diameter.

Vessel-ray pit-pairs half-bordered; opposite or alternate, with rounded or irregular to normal pits to scalariform pit-pairs; normal pits average 10 μ in diameter while the scalariform may reach a length of 30 μ.

Wood parenchyma lacking.

Wood rays heterogeneous II A to heterogeneous II B; 9 to 16 per mm., average 13. Multiseriate rays generally 3 to 4 seriate; average 762 μ in height and 31 μ in weight. Sheath cells present. Yellowish-brown contents few to abundant. Uniseriate rays very variable in height.

Wood fibers extremely short to medium-sized, average 692 μ in length (S.E. 11 μ, S.D. 140 μ); middle diameter average of 19 μ and wall thickness of 3 to 4 μ. Pits bordered; round to oval; 2 to 3 μ in diameter; with lenticular, included apertures or slitlike, extended apertures. Fibers short-tapering. Septate, nonseptate, and substitute.

Echinocarpus Bl.

Genus of three species distributed in Australia. Description based on three specimens of *E. australis* Benth.

Growth rings indistinct or lacking.

Pores round or oval to slightly angled; 6 to 12 per square mm., average 9; tangential diameter range from 91 to 183 μ, average 122 μ (S.E. 1.80 μ, S.D. 16 μ); pore walls average 4 μ in thickness. Pores mostly solitary (52 per cent) and in radial multiples of 2 to 3 (41 per cent), the remaining in tangential pairs or clusters of 3 to 6 pores; evenly distributed.

Vessel members moderately short to medium-sized, average 463 μ in length (S.E. 3.59 μ, S.D. 62 μ); perforation plates simple, transverse to oblique. Gum deposits and tyloses occasional.

Intervessel pit-pairs round or oval and polygonal; 8 to 10 μ in diameter; apertures lenticular, included, frequently coalescing.

Vessel-ray pit-pairs half-bordered; 8 to 25 μ in diameter or length; apertures large, and of the same shape as the pit outline.

Vessel-parenchyma pit-pairs half-bordered; irregularly rounded to ovate; 8 to 20 μ in diameter or length; apertures lenticular, included.

Wood parenchyma paratracheal, paratracheal-banded, and diffuse. The paratracheal parenchyma forming a uniseriate or biseriate sheath about the pores. Paratracheal-banded parenchyma forming zones which are irregularly 1 to 9 seriate. Diffuse parenchyma occurring as isolated cells or small groups in the vicinity of the pores. Parenchyma cells average 23 μ in tangential width and 143 μ in length. With or without contents. Parenchyma cells frequently become very much enlarged and appear on the cross section as small angular vessels which are about 45 μ in diameter. These cells are very conspicuous on all sections and appear to be a constant feature of this wood.

Wood rays heterogeneous II A; 6 to 12 per mm., average 9. Multiseriate rays 2 to 4 seriate; average 778 μ in height and 45 μ in width. Uniseriate rays average 309 μ in height. On the radial section the cells of the wide rays are radially elongated and the marginals are square or erect.

Wood fibers moderately short to moderately long, average 1,172 μ in length (S.E. 15 μ, S.D. 180 μ); middle diameter average of 23 μ and wall thickness of 6 μ. Pits bordered; oval; 8 μ in diameter; with extended, slitlike apertures.

Wood samples: Minnesota No. 1301; Syracuse No. 429/7035; Yale No. 19450.

DISCUSSION

By interpreting the anatomical data given for each genus in light of the lines of structural specialization in the introduction, together with a consideration of the facts from floral morphology, certain conclusions can be drawn concerning the phylogenetic relationships of the tribes and genera studied in this investigation.

The phylogenetic relationships expressed in this bulletin are not, of course, considered to be final. They merely represent the authors' conclusions based on evidence at their disposal at the present time. Further evidence from the fields of cytology, paleobotany, anatomy, and taxonomy may alter considerably the conclusions reached in this investigation.

Elaeocarpaceae

The family Elaeocarpaceae, up to 1895, consisted of a series of tribes which were considered to be a part of the Tiliaceae. This view was held for a long period of time, and, since it was considered a much reduced group, by many phylogenists it was placed in the highest position within the family Tiliaceae. Although most taxonomists recognized the Elaeocarpaceae as quite distinct and generally considered it as a subfamily, suborder, or distinct series, no attempt was made actually to segregate the group from the Tiliaceae. This group was finally segregated in 1895 by Engler and Prantl and was placed in the primitive position before the Tiliaceae. This arrangement has been generally accepted but the various systems in which it is included within the Tiliaceae were still in vogue as late as 1936. Edlin, in his study of the various groups of the Malvales, favors the replacement of the Elaeocarpaceae within the Tiliaceae but places it before the other tribes of that family.

The evidence from wood anatomy substantiates the arrangement of Engler and Prantl; that is, the segregation of the Elaeocarpaceae from the Tiliaceae and making it a separate and distinct family.

Practically all the characters of the Elaeocarpaceae point to a primitive type of structure and, in brief, are as follows: long vessel members; opposite and transitional to scalariform lateral pitting of the vessel members; oblique perforation plates which are mostly simple but show vestiges of the scalariform condition; parenchyma generally lacking; and wood fibers which are very tracheidlike in cross section. The only feature which might point to an advanced character is the presence of septate wood fibers

in most of the genera examined. The Tiliaceae, in contrast, possess none of the features enumerated above. The genus *Echinocarpus* is of special interest in this connection since it exhibits none of the characters mentioned for the Elaeocarpaceae. In fact, all of its characters are those of the Tiliaceae. This genus has either the status of a genus or of a section under the genus *Sloanea,* depending upon what system is under consideration. Most phylogenists consider it to be a section under *Sloanea* but Bentham and Hooker raise it to the rank of a genus under the tribe Sloanieae. The woods of the two genera are so different that it would appear unwise to retain them within the same tribe. The wood of *Sloanea* exhibits the most primitive features of the Elaeocarpaceae while *Echinocarpus* shows a definite trend toward *Erinocarpus* of the Tiliaceae. *Echinocarpus* may well be the connecting link between the Elaeocarpaceae and the Tiliaceae, but until all the woods of Elaeocarpaceae have been collected and studied, assumptions may prove very misleading. The authors do not favor the removal of *Echinocarpus* from the Elaeocarpaceae since its floral characters are those of the latter family, and, moreover, the authors are reminded of the fact that similar combinations of anatomical characters may occur in families which are widely separated as to systematic position. Mention may be made of the remarkable resemblance between the xylem of *Maclura aurantiaca* Nutt. of the Moraceae and the xylem of *Robinia pseudoacacia* L. of the Leguminosae. Thus if the anatomists did not take into consideration the facts from floral morphology, some very curious anomalies would result.

The following arrangement of the tribes and genera of the Elaeocarpaceae was arrived at using only the features of the secondary xylem. The arrangement of Engler and Prantl is reproduced here for purposes of comparison.

The genera marked with an asterisk were not available for study at the present time.

ELAEOCARPACEAE

Wood Structure	Engler and Prantl
I. Elaeocarpeae	I. Elaeocarpeae
1. *Sloanea*	1. *Elaeocarpus*
2. *Elaeocarpus*	2. *Sloanea*
3. *Echinocarpus*	3. *Crinodendron*
**Crinodendron*	4. *Dubouzetia*
**Dubouzetia*	5. *Antholoma*
**Antholoma*	
II. Aristotelieae	II. Aristotelieae
4. *Vallea*	6. *Vallea*
5. *Aristotelia*	7. *Aristotelia*

The tribe Elaeocarpeae is placed in the primitive position because of its long vessel members and solitary arrangement of pores. The Aristotelieae, on the other hand, has vessel members which are much shorter and the pores are mostly in radial multiples and clusters or chains.

Sloanea is undoubtedly the most primitive member of the family. The features which place it in this position are as follows: pores angular in cross section; intervessel pit-pairs opposite; vessel-ray pit-pairs transitional or scalariform; tertiary spirals lacking. *Elaeocarpus,* in contrast, possesses pores which are round or oval, alternate intervessel pit-pairs, normal pit-pairs between the vessels and rays; tertiary spirals are present in some species. *Echinocarpus* is retained in this tribe, but placed after *Elaeocarpus* since the other three genera of this family were not studied.

Vallea and *Aristotelia* possess practically the same features except that *Vallea* has longer vessel members and scalariform lateral pitting—features which place it before *Aristotelia.*

The proposed arrangement of the Elaeocarpaceae is essentially that outlined by Engler and Prantl; the prominent exceptions being that *Sloanea* is placed before *Elaeocarpus* and that *Echinocarpus* is regarded as a genus and not as a section under *Sloanea.*

Tiliaceae

Ever since the original designation of the four principal tribes of the Tiliaceae by Bentham and Hooker in 1862, the tribe Brownlowieae has remained in the primitive position within the family, but the other three tribes have been shifted somewhat by subsequent taxonomists.

The tribe Brownlowieae is separated from the others primarily on the basis of the calyx which is partially united and 3- to 5-lobed at the apex. For the separation of the remaining three tribes, Bentham and Hooker use the character of petal insertion to separate the Grewieae from the Tilieae and the tribe Apeibeae is separated from the latter two tribes on the basis of the number of ovary chambers and type of fruit.

Burret, considering the tribes as proposed by the older taxonomists to be too heterogeneous, proposed 16 tribes distributed among three subfamilies. Here we find the genera generally included under the Brownlowieae, under the subfamily Brownlowioideae, this subfamily being separated from the other two subfamilies on the basis of the calyx as in the previous systems. The subfamily Tilioideae contains 10 tribes, some of which are

separated on the basis of characters which appear to have little phylogenetic significance. On the whole, the characters used in the delimitation of the tribes are very good.

In surveying the characters used for the separation of the principal groups of this family, one is struck by the apparent difference of opinion regarding the direction of specialization of these features. Among the principles adopted for the classification of flowering plants, notably those of Bessey, Hutchinson, and Wettstein, are noted the following conditions: (a) the dioecious condition is probably more recent than the monoecious condition; (b) free petals or sepals are more primitive than connate petals or sepals; and (c) many carpels precede few carpels. According to the above principles, the tribe Brownlowieae should be regarded as an advanced group on the basis of its united calyx parts. In addition, this tribe has several genera which are dioecious, a feature which should further help to remove this tribe from its supposed primitive rank. The Apeibeae, which is characterized by a many-chambered ovary, would be reduced to a much lower level on the basis of the principles stated above.

On the basis of the structure of the wood, the following arrangement of the Tiliaceae is proposed. The disposition of the genera into the following groups is remarkably like that proposed by Burret and in the discussion which follows this outline, the anatomical arrangement is compared with that of Burret. The various groupings are not given tribal names since they vary at times from the original designation by Burret. Only the genera which were actually studied are considered in this outline.

TILIACEAE

Group I
1. *Althoffia*
2. *Trichospermum*
3. *Belotia*

Group II
4. *Honckenya*
5. *Triumfetta*
6. *Entelea*
7. *Apeiba*
8. *Heliocarpus*
9. *Erinocarpus*

Group III
10. *Microcos*
11. *Colona*
12. *Goethalsia*
13. *Luehea*

Group IV
14. *Grewiopsis*
15. *Desplatsia*
16. *Glyphaea*
17. *Duboscia*

Group V
18. *Mollia*
19. *Luehopsis*

Group VI
20. *Grewia*
21. *Vinticena*

Group VII
22. *Tilia*
23. *Schoutenia*
24. *Chartocalyx*

Group VIII
25. *Pentace*
26. *Diplodiscus*
27. *Brownlowia*

Group IX
28. *Berrya*
29. *Christiania*
30. *Carpodiptera*

Group I, the Trichospermae of Burret, is placed in the primitive position for the following reasons: (a) long vessel members (average for group of 597 μ); (b) pores thin-walled and quite evenly thickened; (c) high percentage of solitary pores (75 per cent); (d) long wood parenchyma cells; (e) large intervessel pit-pairs; and (f) a small fiber-vessel length ratio (2.30).

Since the term "fiber-vessel length ratio" is used here for the first time, a word of explanation is in order. It has already been shown that *(4, 26)* the length of the vessel members is approximately the same as that of the cambial initials from which they were derived, and it is therefore permissible to assume that it is also the original length of the fiber initials. Chattaway *(33)* has found that the mature fibers may be from 1.1 to 9.5 times their original length, but the greater elongations only occur where the cambial initials are short. Where the cambial initials are long, the fibers are rarely more than 1.5 times as long as the initials. It thus appears that the greater proportional extension of the fibers is also a feature of the more specialized woods. The ratio is derived by dividing the average fiber length by the average length of the vessel member.

Within group I, *Althoffia* is made the most primitive member since it possesses the longest vessel members, a very high percentage of solitary pores, a very low fiber-vessel length ratio, and wood rays of type II A. The highest member is *Belotia* with the shortest vessel members of this group, abundant diffuse parenchyma in contrast to the very sparse parenchyma in the other two members, rays of type II B which are regularly to irregularly storied.

Burret makes *Trichospermum* the lowest member of his tribe on the basis of the number of ovules per carpel. *Trichospermum* has 25 to 50 ovules per carpel while *Belotia* and *Althoffia* possess 12 to 16. *Althoffia* is placed above *Belotia* because it has 3 to 5 carpels while *Belotia* has only 2 carpels. *Trichospermum* has 2 to 3 carpels. A sequence read on the basis of carpel number would follow from *Althoffia* to *Trichospermum* to *Belotia*. Such a sequence would then be like that which is read from the structure of the woods of this group.

Group II consists of the members of three of Burret's tribes which are: the Triumfetteae, Sparmannieae, and the Apeibeae; his sequence reading in the order given. Most of the genera included under these tribes have shrubby members and apparently for this reason he has placed these tribes in the highest position within the family. Of these three tribes, Apeibeae has a many-

chambered ovary while the remaining tribes possess an ovary which is 2- to 8-chambered.

This group is made up mainly of members which possess a very thin-walled type of parenchymatous tissue which is pithlike in character. The primitive genus *Honckenya* does not possess this peculiar type of tissue but appears to be so closely related to the next member of the series where this tissue is first observed that it rightly deserves the primitive position in this group. This tissue first appears in *Triumfetta* and as it becomes more abundant in the succeeding members of the series it is accompanied by the following changes: (a) decrease in length of the wood parenchyma cells; (b) change in shape of the pores from angular to round or oval in cross section; (c) an increase in the fiber-vessel length ratio (from 1.23 to 4.55); (d) change in ray structure from heterogeneous I to heterogeneous II B; and (e) an increase in the pore wall thickness. This group is advanced over group I in the following respects: (a) decrease in vessel member length (average for group of 416 μ); (b) thicker-walled pores; (c) smaller percentage of solitary pores (60 per cent); and (d) a higher fiber-vessel length ratio.

Honckenya was placed in the primitive position on the basis of its angular vessels, thin-walled pores, very low fiber-vessel length ratio, and wood rays which are heterogeneous type I. *Triumfetta,* the next member, although still possessing angular pores, has pore walls which are somewhat thicker and its fiber-vessel length ratio is more than double that of *Honckenya.* In addition, its wood rays are heterogeneous I and heterogeneous II A. The third member of the series, *Entelea,* is very much like *Triumfetta* but its rays are only heterogeneous II A and its fiber-vessel length ratio is higher. The next two members of the series are identical in many respects and differ only in the size and shape of the intervessel pit-pairs and the cells of the thin-walled tissue, respectively. In *Heliocarpus* the intervessel pit-pairs are 8 to 12 μ in diameter while in *Apeiba* they are 5 to 8 μ in diameter; in *Heliocarpus* the cells of the thin-walled tissue are vertically elongated and polygonal in cross section while in *Apeiba* the cells are radially elongated. The secondary xylem of these two genera has apparently reached about the same evolutionary level but *Apeiba* appears to be more closely related to *Entelea* and for that reason the sequence reads as it does. *Erinocarpus* is undoubtedly the highest member of the series. This genus has a fiber-vessel length ratio of 4.55 and in addition possesses paratracheal-banded parenchyma which is a definite step over the other members of

the group. All of the other members possess either reticulate parenchyma or, in the case of the lowest member, none at all.

Group III is made up of the members of Burret's Coloneae and two additional members, the genus *Microcos* from his tribe Grewieae and the genus *Luehea* from his tribe Lueheeae. All of the members of this group possess abundant reticulate parenchyma and are alike in many other respects.

Microcos, the primitive member of the series, has the longest vessel members, the smallest fiber-vessel length ratio (2.60), and rays which are unstoried and heterogeneous II A and II B. *Colona,* the next member of the series, has shorter vessel members than *Microcos* as well as a higher fiber-vessel length ratio, but the main point of divergence is in the wood rays which are storied and entirely heterogeneous II B in *Colona.* In *Goethalsia* the rays are storied as in *Colona* but the fiber-vessel length ratio is higher and the vessel members are shorter as well as smaller in diameter. *Luehea* possesses the most advanced features of the series. Its vessel members are short, its fiber-vessel length ratio is 4.46, and its rays are all storied and are heterogeneous II B and homogeneous I. Sheath cells are present in all the members of the group and tile cells are lacking only in the genus *Goethalsia.*

Group IV consists of four African genera and appears to be an offshoot of *Microcos* which extended westward across Africa. *Glyphaea* is included under the Apeibeae in all the systems examined, but on the basis of the secondary xylem bears no relation whatsoever to the members of that group or its affinities. Its wood structure agrees perfectly with the woods of this group and has been placed there accordingly. This group forms a homogeneous group as does group III and the principal features indicating specialization are the wood rays and the pitting between the vessels and wood rays and wood parenchyma. *Grewiopsis* is made the lowest member of the series because it has rays which are not storied, the pitting between the vessel members and wood rays is normal, and, in addition, sheath cells and tile cells are present. *Desplatsia,* the next member of the series, has its uniseriate rays storied, but as in *Grewiopsis,* the pitting is normal and tile and sheath cells are present. *Glyphaea* has uniseriate storied rays, but tile cells are lacking and it has unilaterally compound pitting between the vessels and ray cells. *Duboscia,* the highest member, has all its rays storied, unilaterally compound pitting, but lacks both tile and sheath cells.

Group V, which is essentially the Lueheeae of Burret with the exclusion of the genus *Luehea,* comprises two genera which ap-

pear to have *Luehea* for an ancestor. Both members possess paratracheal-banded parenchyma and heterogeneous II B or homogeneous I wood rays, but *Mollia* appears to be the more primitive of the two genera. *Mollia* has the lower fiber-vessel length ratio and its low rays are not storied, while in contrast, *Luehopsis* has the higher fiber-vessel length ratio and its low rays are storied. *Luehopsis* possesses the additional feature of unilaterally compound pitting. Burret makes *Mollia* the highest member of this group on the basis of its two-carpeled ovary; *Luehea* and *Luehopsis,* both with 5 carpels, are the lowest members. This group is little if any advanced over group IV but the two groups appear to be at about the same evolutionary level.

Group VI, the Grewieae of Burret with the exclusion of the genus *Microcos,* shows the following advances in specialization over the preceding groups: (a) very short vessel members; (b) a decrease in the length of the wood parenchyma cells; (c) relatively high fiber-vessel length ratio; (d) tile cells of the *Pterospermum* type; and (e) low uniseriate rays which are storied. On the evidence derived from one sample of *Vinticena,* this genus would be more advanced than *Grewia,* but until more woods of this genus are available the status of this group must remain tentative. The genera included within the Grewieae have caused much confusion among themselves as well as having accumulated a great deal of synonymy. On the basis of the wood they appear to be clear-cut genera, but on the basis of the floral structures they appear to be very difficult to distinguish. Much of this confusion can be traced to Linnaeus who first considered *Grewia* and *Microcos* to be distinct genera but later united them under *Grewia.* This change had been accepted by nearly all botanical authorities until Burret, in 1926, restored *Microcos* to generic rank together with *Vinticena.* Burret bases his classification largely on differences in the stigma, which is simple and apical in *Microcos,* but dilated or lobed in *Grewia,* and on the fruit, which is elobate in *Microcos* but nearly always more or less lobed in *Grewia. Grewia* is further separated from *Vinticena* on the basis of the number of ovules per carpel, there being generally 2 to 6 ovules per carpel in *Grewia* and 10 to 40 per carpel in *Vinticena.* These distinctions are claimed to be quite definite.

Investigation of the wood indicates a close relationship between Burret's rearrangement of the genus and one based upon the structure of the wood. Of the material of *Grewia,* all specimens with the *Durio* type of ray cells are species that Burret refers to *Microcos,* while those with the *Pterospermum* type of ray cells are

species he considers to be true Grewias. An easier method of determining whether a wood sample belongs to *Grewia* or *Microcos* is the measurement of a very small number of vessel members. Vessel members with an average length in the vicinity of 260 μ would belong to *Grewia* while those with a length of about 575 μ would belong to *Microcos*. This same procedure can be applied to twigs of herbarium material, in which case *Grewia* would average about the same as for the mature wood, while *Microcos* would average about 450 μ in length. This method would hold if it were known that the wood specimens were either of the two genera in question, but if wood of *Vinticena* was also present it would be identical with *Grewia*.

Group VII is considered to be the highest of the series which includes all the genera possessing a calyx composed of separate sepals. The reasons for this basis are: (a) high vessel-fiber length ratio; (b) tertiary spirals present in two genera; (c) a lack of either tile cells or sheath cells; and (d) multiseriate rays which are essentially homogeneous.

Burret's tribe contains only *Tilia* and *Schoutenia*, but he reduces the genus *Chartocalyx* to synonymy under *Schoutenia*. *Chartocalyx* had previously been considered a member of the Brownlowieae. The wood structure substantiates Burret's transfer of this genus but not the reduction of the genus to synonymy because the wood is quite different and easily distinguished from *Schoutenia* by the presence of storied rays which are lacking or very indistinct in *Schoutenia*. Both *Tilia* and *Chartocalyx* possess tertiary spirals, but *Tilia* is considered the primitive member of the group because of its angular pores, small fiber-vessel length ratio (2.36), and very high rays. *Schoutenia,* the middle member, has round or oval pores, a fiber-vessel length ratio of 4.09, shorter rays, and a higher percentage of pores which are in radial multiples. *Chartocalyx,* the highest member, has the shortest vessel members, the highest fiber-vessel length ratio (5.29), and rays which are heterogeneous II B to homogeneous I and uniform in height and storied. The characters of this genus are in many respects those of *Carpodiptera* and *Christiania* of Group IX but differ in the lack of unilaterally compound pitting. On the basis of the wood structure this genus would appear to be the intermediate between the two main divisions of this family, that is, the synsepalous tribes and the aposepalous tribes.

Groups VIII and IX are essentially the tribe Brownlowieae of Bentham and Hooker and subsequent taxonomists, and the subfamily Brownlowioideae of Burret. The two groups as a whole

have several distinguishing features in common; these are: (a) storied structure; (b) a high percentage of pores in radial multiples; (c) rays heterogeneous II B to homogeneous I; (d) unilaterally compound pitting; and (e) a high fiber-vessel length ratio.

Group VIII, the more primitive of the series, is placed at the top of the tribe by Burret on the basis of the flowers which are perfect in contrast to the perfect and dioecious condition existing in the following group. The members of group VIII, *Pentace, Diplodiscus,* and *Brownlowia,* have in common the feature of reticulate parenchyma and unilaterally compound pitting. The sequence is read from *Pentace* to *Brownlowia.*

Group IX, the highest of the entire family, is characterized by paratracheal-banded parenchyma and a combination of normal and unilaterally compound pitting. The members of this group have a very high fiber-vessel length ratio (average 5.42), very short vessel members, very low, 1 to 3, seriate wood rays, and wood parenchyma cells which are smaller both in width as well as in length. Burret makes this the most primitive tribe of the family on the basis of the genera, retaining the dioecious condition. From the structure of the wood the sequence is read from *Berrya* upward, *Carpodiptera* and *Christiania* being placed in the highest position because their woods are the most advanced of the family.

GENERAL CONCLUSIONS

It is apparent from a study of the woods of this family that the features which show specialization according to the principles of plant classification are correlated with a high degree of specialization in the organization of the secondary xylem. Thus, after the rearrangement of certain questionable groups, the classification of the taxonomists and the phylogenetic scheme of the anatomists show surprising agreement.

At this time it must be admitted that the use of the anatomical method in phylogenetic studies has certain definite limitations. It has been pointed out before that similar combinations of anatomical characters may occur in families which are widely separated as to systematic position. Therefore, if the anatomists were to build up a phylogenetic system on the basis of anatomy alone, some rather strange results would ensue. Because of this convergent evolution, and also because of a parallel evolution in stem structure, the anatomist must proceed with caution.

The anatomist can, however, make certain definite contribu-

tions to problems of phylogeny if he uses the various systems built upon the basis of floral morphology as a background for his work.

SUMMARY

1. A study of 578 specimens, representing 206 species and 37 genera, revealed a marked similarity in the structure of the secondary xylem of the great majority of the investigated genera and a decided diversity in the anatomy of the others.

2. The woods of the various genera are described.

3. The fiber-vessel length ratio was found to have considerable phylogenetic significance.

4. Unilaterally compound pitting appears to be an advanced feature which appears sporadically in the aposepalous tribes and reaches its culmination in the synsepalous tribes where it forms a constant feature.

5. Evidence from wood structure substantiates the system of Engler and Prantl in the segregation of the Elaeocarpaceae from the Tiliaceae as well as the disposition of the genera and tribes of the former family.

6. The Elaeocarpaceae are more primitive than the Tiliaceae.

7. *Sloanea* is considered the most primitive member of the Elaeocarpaceae.

8. *Echinocarpus* should be regarded as a distinct genus and not as a section under the genus *Sloanea.*

9. The family Tiliaceae comprises at least nine distinct groups on the basis of wood structure and these groups most nearly approximate the tribes as proposed by Burret.

10. The shrubby members of the family appear to be more primitive than the arborescent forms.

11. The Trichospermae, as designated by Burret, is considered to be the most primitive group.

12. The Brownlowieae, in contrast to any of the previous systems, appears to be the most highly advanced group of the family.

13. *Chartocalyx* and *Grewiopsis* should be regarded as distinct genera and not reduced to synonymy under *Schoutenia* and *Desplatsia,* respectively.

14. *Grewia* and *Microcos* are distinct genera which have deviated greatly in the organization of their woods. The status of *Vinticena* is still tentative.

15. In general, the evolution of floral structures seems to be

correlated with the evolutionary development of anatomical structures.

16. There is every indication that the study of anatomy will be of great value in the establishment of a natural classification of the angiosperms.

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